

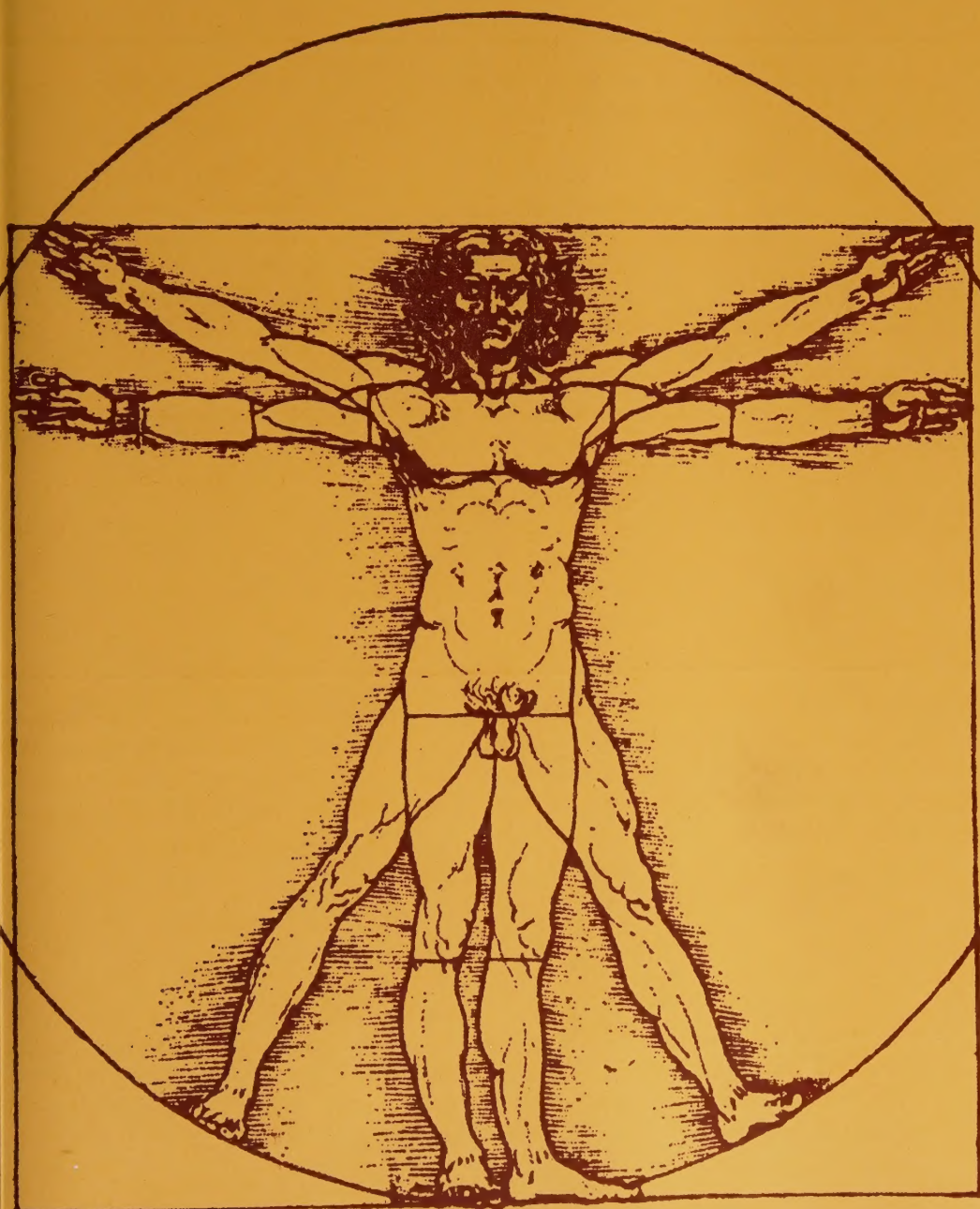
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Special issue 1974. Professor Duane M. Rumbaugh, with the cooperation of Dr Leonard A. Rosenblum, will be organizing this year's special issue which will be devoted to "Comparative Behavioral Primatology". Those interested in this topic should write to Professor Duane M. Rumbaugh, Department of Psychology, Georgia State University and Yerkes Primate Center, Emory University, U.S.A.

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Alberto Oliverio

*Laboratorio di Psicobiologia e
Psicofarmacologia, Via Reno, 1,
00198, Roma, Italy*

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Evolutionary Mechanisms in Behaviour: An Intraspecific Genetic Approach

The study of the evolutionary mechanisms in behaviour and of the biological grounds of individual variability may be based on the comparative phylogenetic approach or on an intraspecific genetic analysis. The discontinuous behavioural progression evident across species is due to the assumption that the phylogenetic "scale" may be adopted in place of the phylogenetic trees and to the fact that today's existing species have evolved in parallel and may not be used to represent an evolutionary sequence. However, despite the existence of different motor and perceptual abilities the comparative approach has shown that many analogies exist between some basic brain mechanisms across species.

The existence of outstanding individual differences within the same species must be regarded as a powerful potential tool since quantitative differences between the behaviours of different individuals belonging to the same species might later result in qualitatively different phenotypes. By using different strains and mutations of mice and different genetic approaches it has been possible to assess the mode of inheritance, to calculate estimates of heritability and of the number of segregating units for different behavioural traits ranging from avoidance to maze learning and activity. The existence of clear genetic correlations between some of these behavioural patterns has also allowed the identification of some single-gene mutants affecting these traits and the characterization of a gene responsible for a major effect on activity. This psychogenetic approach shows that there are behaviour differences which are the products of evolutionary adaptive processes and that the knowledge of the genetic systems that underlie these differences is a basic step for understanding the brain mechanisms in Man.

The existence of individual and group differences in the behaviour of animals and humans is too evident to escape notice. As a result of Darwinian views, it has become obvious that phyletic variation has been, and continues to be, dependent upon intra-specific variability since within groups, differences form the raw material of evolution. This concept was clearly enunciated by Darwin who was so impressed by the morphological and behavioural differences existing between several groups of birds of the species *Geospiza* living in the Galapagos islands, to state that "one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends" (Darwin, 1839). However, acceptance of the existence of intraspecific behavioural variation needed a long process of rejection of many previously held concepts. This process, which required the replacement of typological thinking by population thinking has been defined by Mayr (1963) as "the greatest conceptual revolution that has taken place in biology".

The roots of typological thinking go back to Platonic philosophy and to the theory that admitted the existence of prototypes, or ideas, the individual persons, animals or objects being instead considered as pale shadows of their ideal "types". To Aristotle the realization of the ideal form involved a single architectonic plan in which the living—and non-living—bodies formed a "Great Chain of Being" ranging from a lesser to a greater perfection (Lovejoy, 1936). The duality of mind and body, with Man as the unique being provided with a metaphysical mind, was the ground for a strong opposition

Table 2

Brain weight and encephalization coefficients in different species

Brain weight (g)		Ratio brain weight/body weight		Ratio brain weight/ $\sqrt{\text{body weight}}$	
Whale	7000	Man	2.17	Man	2.81
Elephant	5500	Mouse	2.04	Elephant	1.24
Man	1360	Cat	0.94	Gorilla	0.76
Gorilla	400	Gorilla	0.65	Chimpanzee	0.74
Chimpanzee	300	Chimpanzee	0.54	Cat	0.32
Seal	225	Elephant	0.18	Whale	0.26
Cat	30	Whale	0.01	Mouse	0.07
Mouse	0.4				

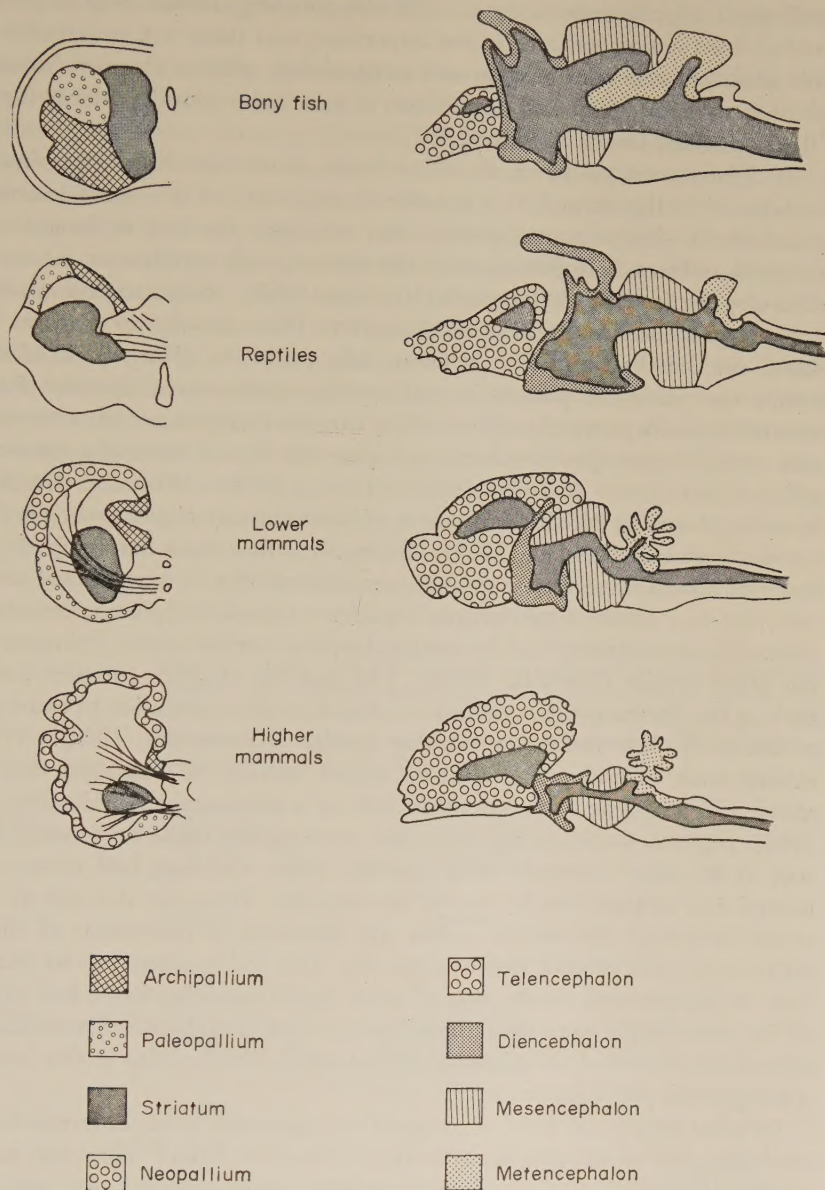
The same problem exists when one tries to correlate brain size with phylogenetic variation in behavioural repertoires. Since brain weight *per se* is a crude estimate, different attempts have been made to obtain a value more related to the "intellectual" achievements of the different species. Thus, different coefficients have been proposed, based on the ratio between brain weight and body weight or between brain weight and the square root of body weight (since brain growth is roughly proportional to the square root of body weight) (Table 2). More recently, it has been shown that the brain weight grows more slowly than body weight and that the exponent 0.66 accounts quite well for this difference. This relation is very similar to that existing between the growth of body weight and that of body surface. A new coefficient of encephalization (K) has therefore been proposed in which $K = \text{brain weight/body weight} \times 0.66$. The value of K would be 0.92 in Man, 0.41 in monkeys, 0.29 in non-human Primates and 0.06 in the other mammals. This ratio is not a very consistent estimate since a higher value is evident in monkeys than in non-human Primates, probably due to their larger body size (Chiarelli, 1972).

The hypothesis that the amount of neural tissue is related to the intellectual capacity of the subject has been tested by Rensch (1956) who tried to equate testing conditions to differences in body size and motor abilities. The results suggest in general that large-brained animals perform better and retain for a longer time the acquired information than small-brained animals. More experiments, however, are necessary to confirm these results, as Rensch himself has pointed out. There is in fact a number of findings indicating that as we ascend the phylogenetic tree, the brain has not evolved by simply adding a quantity of functions to the already existing ones but by modifying its structure and patterns of adaptation. That different patterns of learning ability rather than simple neural continuity are at the basis of phyletic differences has been clearly demonstrated by Bitterman (1965). Different species of fish, turtles, pigeons, rats and monkeys were compared in different learning tasks involving spatial, visual probability, and reversal learning. On spatial problems based on reversal or probability learning, turtles, pigeons, rats and monkeys show similar response patterns while fish are clearly different. On visual reversal learning, pigeons, rats and monkeys performed similarly, while fish and turtles were different. On the contrary, monkeys and rats performed alike on probability learning, while pigeons, turtles and fish showed distinct behavioural patterns. This would prove that as we ascend the phylogenetic scale intellectual discontinuity is evident.

What are the organic foundations responsible for the similarities evident in some basic brain processes across species or for intellectual discontinuity along the phylogenetic tree? A number of comparative studies on the role exerted by the different structures of the nervous system on the organization of behavioural activity have demonstrated that a hierarchical organization is responsible for the increasing sophistication in behavioural patterns (Altman, 1966; MacLean, 1970). The most ancient component of the Chordata nervous system, the spinomedullary formation, is involved in a number of innate apsychic activities devoted to maintenance and coordination functions such as visceral, respiratory or circulatory activities and stereotyped patterns such as muscular coordination and locomotion. The mediation of local segmental reflexes is a phenomenon observable from protochordates like the *Amphioxus* to intact or spinal mammals. The brain itself may be divided into three main structural systems corresponding to phylogenetic levels of increasing complexity. The reticular formation, the mesencephalon and basal ganglia (which in mammals form the *corpus striatum*) represent the simplest level of complexity responsible for a number of instinctive activities such as mating, breeding, establishing a territory, imprinting, etc. These formations, which are already evident in reptiles (Figure 1) are in general involved in survival activities and stereotyped behaviours which, in neomammals, are under control by the cortex which evolves in size through the phylogenetic tree (Figure 1). The primitive cortex of the paleomammalian brain, the archipallium, forms the structure of the limbic system, a structure rather stable from an evolutionary point of view in contrast to the neocortex. A number of studies (MacLean, 1970) demonstrate that the limbic system is involved in different types of emotional behaviours, feeding, fighting and self-protection. This has been clearly demonstrated in recent experiments based on the electric stimulation of different brain areas in cats, monkeys and even Man. By means of small electrodes implanted in specific areas of the brain, it is possible to induce rage or sleep, hunger or thirst, running movements or relaxation and even the recall of previous events or an enhancement of memory consolidation processes (Delgado, 1969; Denti, McGaugh, Landfield & Shinkman, 1970). Finally, in higher mammals and Primates the neencephalon assumes, through an expanse network of projection and association areas, the control of highly evolved memory and learning mechanisms and of highly adaptive behaviours. In Primates the encephalic anterior and posterior association areas occupy the largest area while in lower mammals the various sensory systems and the motor area predominate.

Two main implications stem from this brief survey on the comparative organization of the central nervous system: (a) The first is represented by the superimposed role of instinctive processes on the adaptive mechanisms of lower mammals. The second is represented by the analogies existing between some basic brain mechanisms across species. The first point underlines the importance of species specific patterns or instinctive behaviours in learning processes: the animal is not a *tabula rasa* and each species might respond in a different way to the same stimuli. Examples in line with this point are frequent in the literature but some of the most outstanding are given by Breland & Breland (1961). A racoon, for example, may be conditioned to drop a coin in a container to get some food. After a while, however, the animals develop a species specific pattern: they do not let the coin go off but rub and "wash" it for a long time. Similarly, the development of pecking behaviour in birds, of rooting behaviour in pigs, and so on, may interfere with operant conditioning procedures. These examples show

Figure 1. Stages in the evolution of the brain in transversel or longitudinal sections. The progressive increase of the neopallium in relation to the striatum and archipallium (*hippocampus*) is evident in the transversel sections. The longitudinal sections indicate the importance of the mesencephalic and diencephalic structures at the lower phylogenetic levels and the increased role of the telencephalon (cerebral hemispheres) in mammals.



how strong are the innate mechanisms of behaviour and how they interfere with new habits. A progressive evolution in the role of instinctive behaviour and fixed action patterns is evident as we proceed from the "lower" to "higher" species. The behaviour repertoires of different species of monkeys are rather fixed: the behavioural differences are due to the acquisition of new fixed action patterns rather than to the variability of individual adaptive mechanisms. On the contrary, in the most evolved Primates, the role of fixed action patterns is less important, and there is a progressive decrease in the role of dominance relationships and territoriality, while a clear evolution in the mother-child interaction, play and acquisition of new behavioural patterns is evident (Bruner, 1972; Harlow, Gluck & Suomi, 1972).

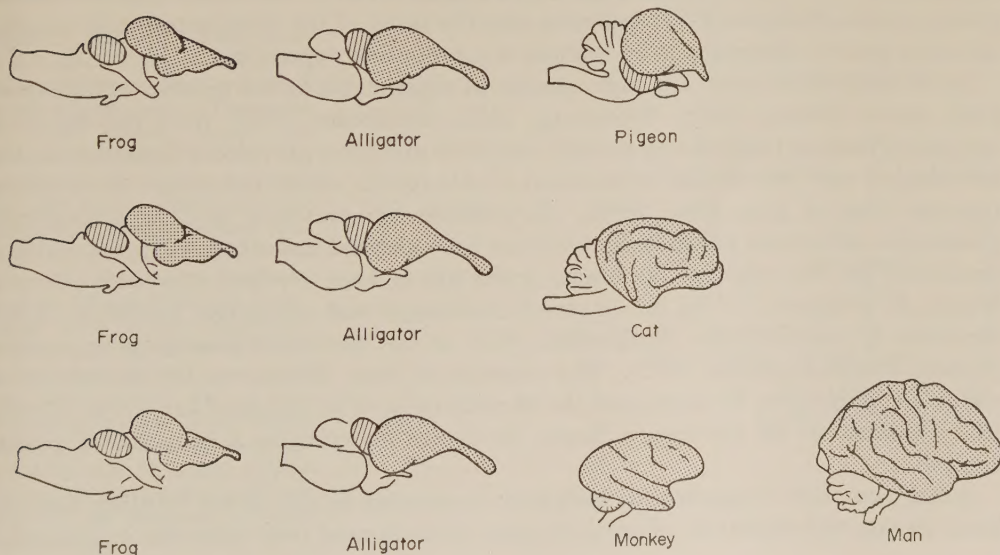
(b) The second point, on the other hand, shows that if the experimental situation is "adapted" to the animal, it is possible to demonstrate that some learning processes are qualitatively similar across species. For example, the rate of formation of active conditioned reflexes is approximately the same in all vertebrates, hence it reflects with difficulty the level of phylogenesis (Voronin, 1962). When more complex learning tasks are adopted such as learning set formation [the capacity to perform a series of tasks based on the discrimination between odd problems (Harlow & Hallow, 1949)] the results show that the process is qualitatively similar across species. Rats, cats, skunks, ferrets or monkeys are characterized by the possibility to perform correctly a number of sets, though some species achieve a higher number of successful consecutive discriminations (Doty, Jones & Doty, 1967; Warren, 1965). With the exception of monkeys, however, learning set discrimination abilities do not show a progressive phylogenetic trend (Hodos & Cambell, 1969). Similarly, other tasks involving the acquisition of a series of conditioned responses show that in reptiles or amphibians the formation of a new link in a chain of movements requires a considerably larger number of trials while mammals are characterized by similar levels of performance. Primates only outperform the other species (Voronin, 1965). The analysis of more complex forms of behaviour such as the "extra-polatory reflexes"—based on the association of cause and effect—gives evidence of clear differences among species (Krushinskii, 1962). While 45-days old infants seem to understand that an object moving in a straight line with a constant speed will reappear from the other side of a screen which hides the stimulus (Bower, 1966), pigeons, ducks, fowls, crows and even rabbits made no attempt to seek for a food tray at the other extremity of a corridor where the food had disappeared after being moved in a straight line in view of the animals. However, if a gap in the middle of the screen informed the animal about the direction of movement of the stimulus, clear differences were evident between species. This information was in fact of no use in the case of pigeons and ducks, was of some importance for fowls and rabbits while birds of the crow family were immediately able to use it and walked around the screen on the side of movement of the stimulus (Krushinskii, 1962). Also in this instance there is not a progressive phylogenetic trend.

Of what help is this kind of comparative approach to an understanding of behavioural evolution and to an analysis of brain functions in Man? How can we explain the discontinuous behavioural progression evident across species? An analysis of imprinting in birds, for example, is a useful approach to the study of adaptation to specific problems of survival but is limited to birds and lends itself with difficulty to generalization with respect to Man (Harlow, Gluck & Suomi, 1972). Imprinting-like phenomena are mostly evident in precocial animals, but are of little help in the study of mother-infant ties in

altricial animals. The comparative approach may be of great advantage in assessing the relationships between the structure of the nervous system, as evident in a given species, and a particular function or in describing the evolution and the adaptation to problems of survival (ethology). On the contrary, most of the comparative studies are not of great help in the reconstruction of specific evolutionary sequences that might help to understand how we have reached a given level of behavioural and neurological sophistication.

One of the main factors limiting the comparative approach is the fact that the representatives of species existing today have evolved in parallel and may not be used to represent an evolutionary sequence (Delius, 1970; Washburn & Harding, 1970). Each of the groups of living mammals has followed its own evolutionary course to its present developmental level. The phylogenetic tree, e.g. the ranking of the animals along a taxonomic hierarchy, does not describe an evolutionary order. On the contrary, a phylogenetic tree is an evolutionary genealogy of living and extinct animals based on paleontological, morphological, physiological, behavioural and biochemical data. The persistence of the phylogenetic-scale concept has been viewed as having a detrimental effect on the development of comparative psychology (Hodos & Campbell, 1969). Thus, the neuroanatomical and neurophysiological comparisons based on series such as the rat, the cat and the monkey are erroneous since rodents, carnivores and Primates have evolved on independent lines and represent today the results of parallel rather than sequential evolution. A neurophysiological or behavioural series based on the frog-alligator-pigeon, the frog-alligator-cat, or the frog-alligator-monkey-Man comparisons is more correct if one wished to study the phylogenetic trees of the birds, carnivores or Primates respectively (Figure 2). Also in this instance, however, we deal with the final steps of different evolutionary patterns.

Figure 2. Stages in the evolution of the brain of birds (top), carnivores (middle) and Primates (lower line). The optic tectum is indicated by vertical lines and the cerebral emispheres by the dotted area. The drawings, on different scales, indicate the increase of the cerebral emispheres in carnivores and mammals.



We know that there are many analogies between the behavioural mechanisms of different species, but the comparative approach faces many problems when one tries to assess the origins and the evolution of a given behaviour. The first problem derives from the different motor or perceptual abilities evident in different species: when single learning tasks are adopted, these differences are not very important but when more complex tasks are used it is difficult to adapt the experimental conditions to the species specific strategies. The second problem is related to the "probabilistic" nature of the phylogenetic tree and to the scarce relationships existing between a given living species and its ancestor (Mayr, 1963). Despite these limitations, the animal model has no substitutes and has proved to be a successful research tool. A number of basic findings, from the action of the psychotropic agents to the role of the mother-child relationships (Harlow & Suomi, 1970), from the effects of maternal deprivation to those of early experience (Denenberg, 1969) or to the effects of handling and early stimulation (Levine, 1967) have been first obtained in different animal species and then successfully applied to Man. The phylogenetic aspects of behavioural evolution are just the starting point in the study of the individual differences in behaviour. They prove that these differences exist, but do not allow a complete analysis nor the possibility of correlating them with structural or biochemical patterns. In order to move a further step and to understand the mechanisms of behavioural evolution within species, comparisons must be assessed.

As pointed out by Schneirla (1966) the existence of outstanding individual differences within the same species must be regarded as a powerful potential tool for these studies. Since understanding behavioural evolution requires knowledge of how natural selection has moulded these behaviours, it is necessary to concentrate more on intraspecies processes than on phylogenetic history, because quantitative differences between behaviours of different individuals belonging to the same species might later result in qualitatively different phenotypes. The meaning of psychogenetics does not consist of a mere extrapolation of some behavioural models from animals to Man, or of an anthropomorphic interpretation of some instructive activities, but of the study of the mode of inheritance of different behavioural patterns of the genes involved and of "mechanism specific" behaviours. The fact that similar genes exert comparable biochemical effects in various animal species (Kalmus, 1971) indicates that the study of the behavioural individuality and of its genetic determinants in animals is a promising approach.

In the most recent years the large number of experiments on the genetics of the laboratory mouse (Green, 1966; Grüneberg, 1952; Medvedev, 1968) have resulted in a number of lines and inbred strains easily available and have provided information on the neurological and behavioural maturation of this species which resembles—in its initial patterns—that of Man (Fox, 1964). In addition, the existence of clear intraspecific phenotypic differences at the brain level has been assessed indicating a large individual variability for the weight of the brain, or the size of some cerebral structures (Wimer, Wimer & Roderick, 1971), the levels of cholinergic and adrenergic mediators (Ebel, Hermetet & Mandel 1973; Eleftheriou, 1971) or the electroencephalographic patterns (Valatx, Bugat & Jouvet, 1972). The existence of these differences, the availability of about 300 single-gene mutants, and the identification of its standard karyotype (Green, 1972) indicate in the laboratory mouse the choice material for a behavioural genetic analysis.

A large number of experiments have been conducted by our group by using different lines, strains and mutations of mice in order to determine their attitudes in a number

of behavioural measures ranging from active and passive avoidance to maze learning and lever-press instrumental learning, from measures of wheel running activity to exploratory behaviour. One of the tests most frequently adopted—active avoidance conditioning in a shuttle-box—seemed to be particularly indicated because of the type and the constancy of the motivation adopted. Staying alert to avoid and escape from predators is in fact one of the basic requirements for the survival of a wild species (Bovet, Bovet-Nitti & Oliverio, 1969). In this test the animals are required to move from one to the other compartment of a double-grid floor cage in order to avoid a shock when a visual or an auditory conditioned stimulus is presented.

As a specific example of the individual behavioural variability evident in a group of genetically heterogeneous, random-bred mice, Figure 3 shows the performance of the animals in the shuttle-box. The behavioural heterogeneity of these mice is clearly evident: the animals were given five 100-trial sessions during five consecutive days. When the mean percent avoidances are plotted according to frequency classes it appears that a rectangular distribution characterizes this population since an equal number of mice present low, high, or intermediate performance levels. This finding indicates clear intrapopulation polymorphism and the presence of a variety of genotypes which yields high adaptedness depending on the environmental conditions.

A possibility to alter the genetic homeostasis of a random-bred population artificially, and to displace the behavioural modality from the distribution previously observed, is to breed the mice selectively for a given trait. Figure 4 shows that after about three generations it was possible to select a line of mice which passed, from the initial level of about 20 % avoidances to a level of 80 % (Bovet, Bovet-Nitti & Oliverio, 1969). This seems to be indicative of the genetic plasticity of the species in relation to this trait and supports the concept that this kind of behaviour is highly adaptive and advantageous for survival in natural environments since intrapopulation polymorphism leads to superior adaptedness in different environments and habitats.

Artificial selection against a given phenotype is a biometric procedure feasible only when it is possible to breed a given number of successive generations in a relatively short period of time. When the animals are characterized by long life spans and late sexual

Figure 3. Frequency distribution of avoidance responses in a group of random-bred mice and in 3 strains of inbred mice. The height of each column shows the number of mice having the avoidance performance shown on the scale below. The rectangular distribution of random-bred mice indicates that individuals characterized by low, intermediate or high avoidance levels are represented with similar frequencies. On the other hand the 3 inbred strains shown in the lower graph are characterized by a very homogeneous range of responding which is low (C57BL/6J), or high (DBA/2J and SEC/1Re) respectively. No overlapping is evident between the responses of these three strains.

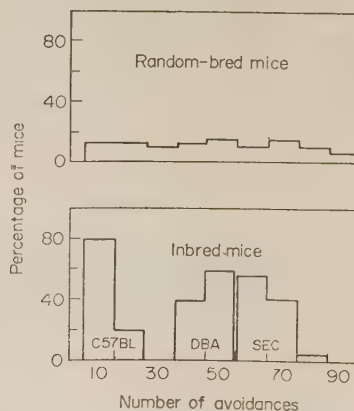
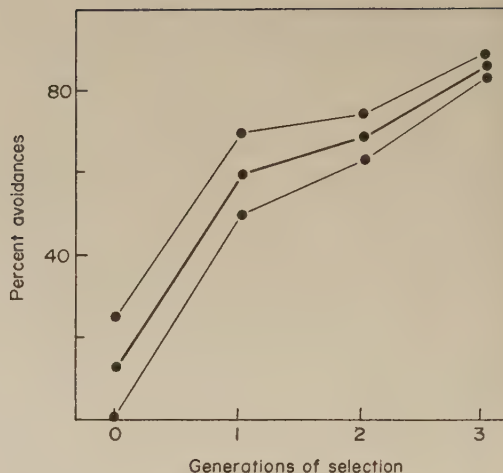


Figure 4. Selective breeding for avoidance learning in the mouse. Each point represents the performance reached at the end of five 100-trial sessions (thick line). Thin lines = fiducial limits of the mean.



maturity as in the case of monkeys, full sib-half sib correlations to the intrasire F_1 progenies of different dams are the most suitable biometric estimate for assessing the heritability of a given trait. This design was successfully applied to a genetically heterogeneous population of mice (Oliverio, 1971). Each of 5 sires was mated to a different group of 10 females. By this means the offspring of each dam was constituted by different full siblings and the total offspring of the 10 dams was constituted by 10 groups of different half siblings. Intrasire breeding brought to a reduction of the offspring's behavioural variability when this was compared to that of its respective groups of dams (Figure 5). In addition to that, the overall performance of the offspring deriving from a given sire was high, low, or intermediate depending on the performance of the sire considered. Estimates of heritability were calculated showing that nearly 50% of the variance among intrasire offspring was attributable to additional genetic causes. Comparable estimates were obtained by using the regression method (intrasire regression of the offspring on dams). In fact, the slope of the regression line indicated that heritability had the value of $h^2 = 0.52$, since the progenies of high-avoiding dams was also characterized by high avoidance levels and that of low-avoiding dams by low performance (Figure 6). Thus, also this experiment shows that differences among mice for this measure of learning ability are conditioned by the genetic traits of the individuals, and that intrasire mating results in a decreased organismic diversity because of an arrangement of the population on a narrower range.

Another versatile possibility in psychogenetics relies on the use of inbred strains of mice. A very large number of these strains is available today, their genetic homozygosity resulting from a number of studies based on different immunological methods. Thirty-nine strains have also been characterized for their alleles for as many as 16 polymorphic loci. The variability among these strains is at least as great as in any single feral population, a large group of inbred strains with unique alleles and no overlapping pedigrees being available as the best group to screen for a hoped-for variant (Roderick, Ruddle, Chapman & Shows, 1971).

Within-strain behavioural homogeneity is clearly evident from an analysis of the avoidance behaviour of two inbred strains of mice trained in a shuttle-box with the same procedure previously described for random-bred animals (Figure 3). On the contrary,

Figure 5. Mean percentage avoidance ($\pm 95\%$ confidence limits of the mean) during sessions 1–5 in five groups (A–E) of DC1 dams and their offspring. [Individual differences are larger in the five maternal populations (circles, white area) than in the corresponding offspring (triangles, dark area).]

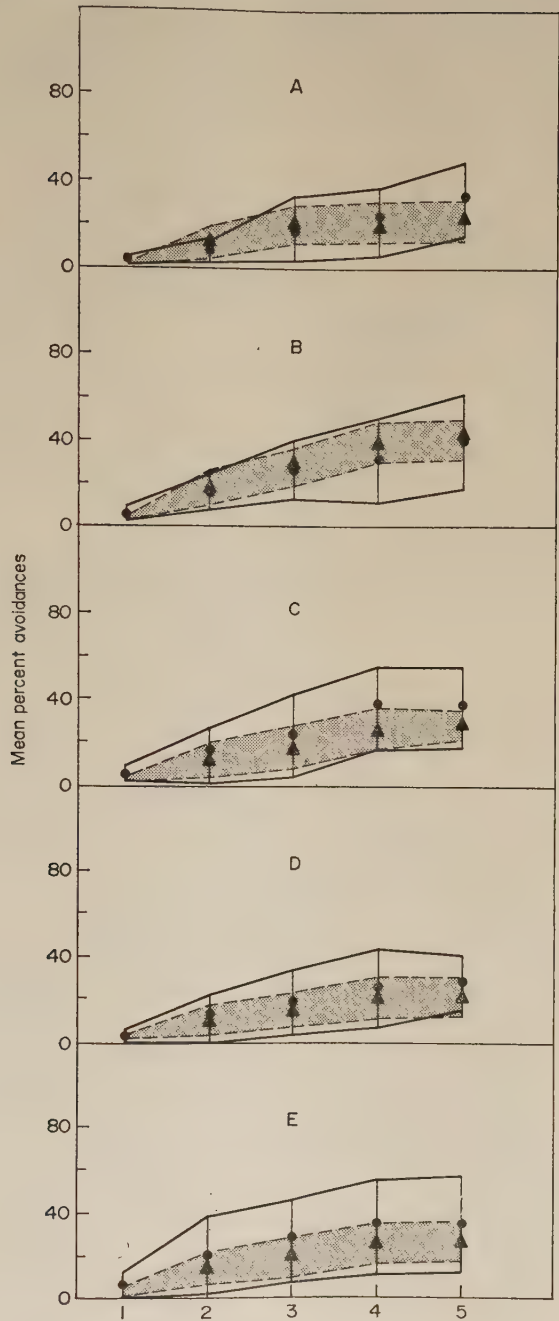
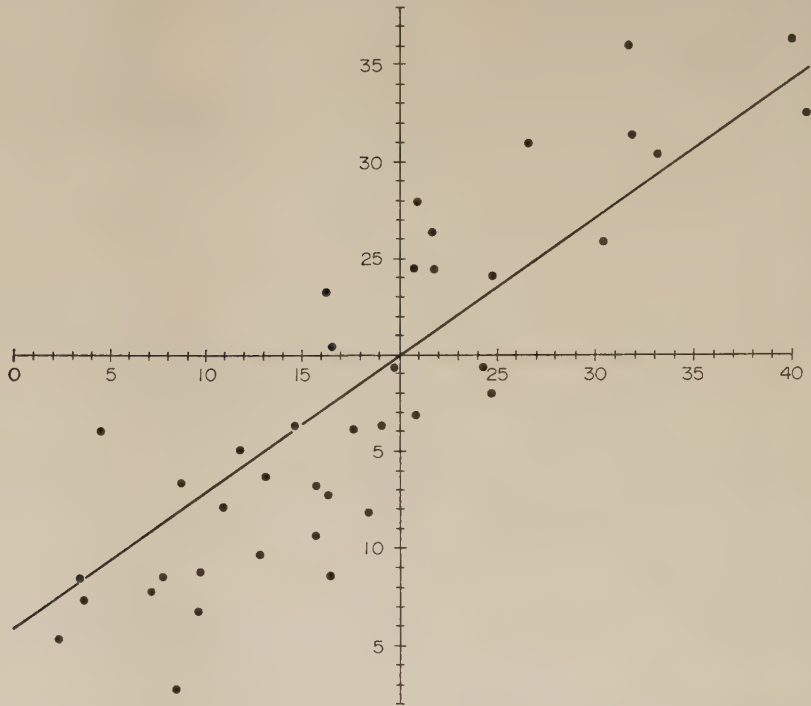


Figure 6. Regression of offspring on dam. Dam values are shown along the horizontal axis, and mean values of offspring along the vertical axis. The axes intersect at the mean value of the performance of all dams and all offspring (Oliverio, 1971).

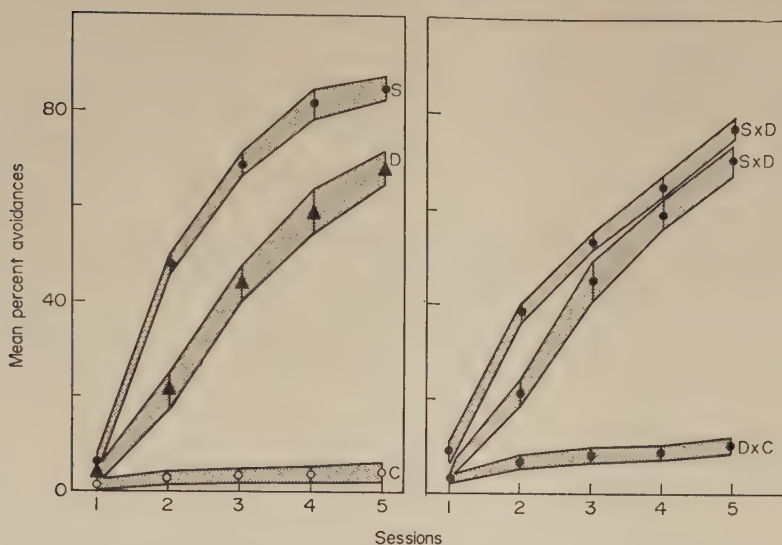


the genetic differences characterizing different inbred strains of mice also result in clear behavioural differences in that various strains of inbred mice attain various avoidance levels. By comparing the overall performance levels reached by nine strains of mice it was evident that three strains performed very poorly (C57BL/6J, C3H/HeJ, and CBA), two (DBA/2J and C57Br/cdJ) attained a very high level of performance, while the rest of them showed intermediate values.

Recently our attention has been focused on 3 different strains of mice with the purpose of conducting a genetic analysis of learning and of some biochemical equivalents of the strain differences. A biometric analysis of avoidance, maze learning and wheel running activity has been conducted in mice belonging to three inbred strains and to their F_1 , F_2 , and F_3 progenies. While two strains (SEC 1/ReJ and DBA/2J) were characterized by high levels of avoidance and maze learning but by low levels of running activity, a third strain (C57BL/6J) attained poor avoidance and maze levels but was very active (Oliverio, Castellano & Messeri, 1972). Three main findings have emerged from the analysis.

(1) The mode of inheritance in a given behavioural measure was shown to depend on the crosses considered (Figure 7). Crossing the C57 strain with the high avoiding-low running SEC mice resulted in SEC-like progeny while crossing with the high avoiding-low running DBA mice yielded an offspring similar to the C57 phenotype. A similar dominance pattern was evident for maze learning, the SEC strain being characterized by the larger proportion of dominant genes in the three tests.

Figure 7. Mean percentage avoidances ($\pm 95\%$ confidence limits of the mean) during sessions 1–5 in three inbred strains of mice and their F_1 offspring. C = C57BL/6J; D = DBA/2J; S = SEC/1ReJ, (Oliverio, (Castellano & Messeri, 1972).

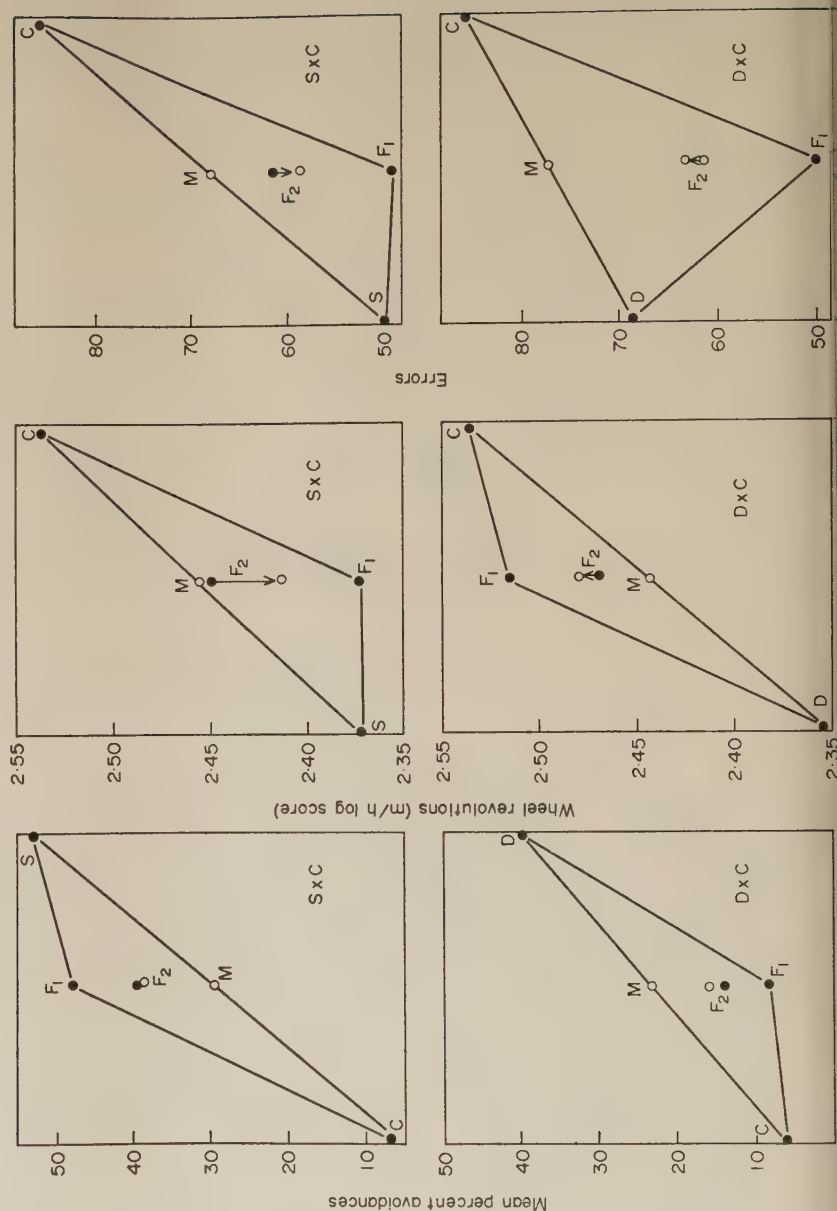


(2) Matherian analyses for F_2 segregation showed that the total F_2 variance (S^2tF_2) contained, in addition to an environmental component (S^2e) a significant genetic component (Figure 8).

(3) Estimates of heritability and genetic correlations were assessed on F_3 mice and their F_2 parents. Estimates of heritability (h^2) based on dam-offspring regressions or on sib correlations were higher for avoidance and maze learning than for activity. The estimates of the correlations between avoidance and activity were negative and large enough to be ascribed to a pleiotropic effect. The existence of significant positive genetic correlations between avoidance and maze learning suggested also that these behaviours were influenced by many of the same genes, though this effect might also be ascribed to linkage effects. Thus, the two $C57 \times SEC$ and $C57 \times DBA$ F_1 hybrid mice were very similar for avoidance, maze and activity patterns to their SEC or C57 parents respectively. Also if these similarities do not determine that the genetic differences affected learning ability in the broader sense, an analogy between the brain mechanisms characterizing each of these hybrids and its dominant parent strain seems plausible. The results of different biochemical estimates indicate clear differences between the brain chemistry of these strains and their hybrids. The poor avoiding strain C57 is in fact characterized by low acetylcholinesterase and cholineacetyltransferase activity in the temporal lobe while higher levels of enzymatic activity are evident in the brains of the high-avoiding DBA and SEC inbred mice (Ebel, Hermeter & Mandel, 1973).

The fact that some of the same genes may be responsible for different behavioural traits gives a higher chance of identifying single-gene substitutions which might possibly affect these behavioural systems. Mutant strains are particularly important for tracing gene-behaviour pathways and for studying "mechanism specific" behaviours (Fuller, 1965). Different mutations on the C57BL/6J background were studied for their effects on avoidance, maze learning and activity. It was particularly interesting to note that

Figure 8. Genetic triangles representing the observed and expected population means in three strains of inbred mice (C, D and S) and their F_1 and F_2 progeny. The mean values for the nonsegregating populations form the corner points of a triangle which is inscribed in a square. The mean measurement for F_1 lies on the vertical line which bisects the square, at a distance d above the midparent (M). The expected means for F_2 (open circles) are at a distance $d/2$ above the midparent. The observed F_2 values are shown in filled-in circles and an arrow points from observed to the expected means. The S strain is dominant over the C strain while D mice are recessive in relation to the C line, (Oliverio, Castellano & Messeri, 1972).



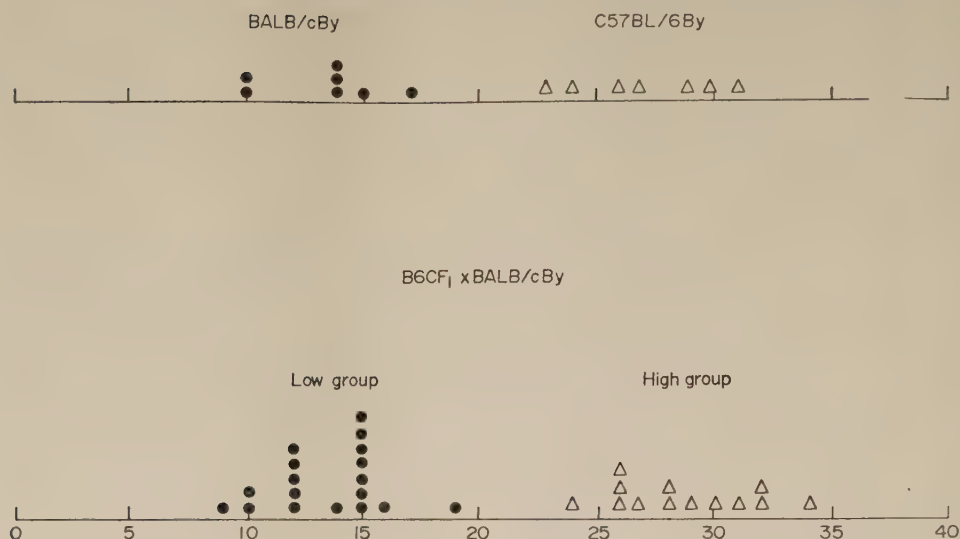
different single gene mutations exhibited avoidance levels higher than that of low-avoiding C57BL/6J normal mice. The higher performance of some mutant strains (albino, underwhite and lustrous mice) seems to be due to a specific effect on behaviour since also maze solving ability was enhanced in these strains (Oliverio & Messeri, 1972). Thus these two behavioural traits seem to be determined by some common psychophysiological mechanisms. The fact that the loci responsible for these behavioural traits are on different linkage groups (at least five) means that recombination to give different phenotypes will occur with a high frequency. The outcome of different phenotypes is responsible for intrapopulation (and interpopulation) variations and for evolutionary changes in behaviour.

A recent and more refined method of genetic analysis based on the strain distribution pattern (SDP) in a set of recombinant inbred strains (RI) (Bailey, 1971) was successfully used in a behavioural study. This type of genetic analysis was developed so that one could determine quickly the probable location of a new gene by matching its pattern of distribution (SDP) among a set of inbred strains. The seven recombinant inbred strains used in this analysis derived from an initial cross of BALB/cBy strain with C57BL/6J mice having then been kept from the F_2 generation by strict inbreeding. This procedure fixes genetically the change recombination of the genes that occurred, though in ever-decreasing amounts, in each succeeding generation after the F_1 . The resulting battery of strains can be looked upon, in a sense, as a replicable recombinant population. The SDPs of distinctive loci (histocompatibility, isozymes, etc.) have been determined in the seven RI strains. The SDP method, therefore, is useful in searching for gene identity, since identical or similar SDPs of any pair of traits indicate possible pleiotropism or linkage of controlling genes. This method was applied to the search of the gene(s) responsible for differences in exploratory activity.

While the BALB/cBy (C) strain was characterized by low exploratory activity, the C57BL/6By (B6) strain and the two F_1 reciprocal hybrids displayed higher exploratory levels indicating dominance of the B6 strain. The RI lines were distributed along either high or low patterns, with absence of intermediate groups: this fact, together with data from backcross $B6CF_1 \times BALB/cBy$ consisting of two distinctive groupings (Figure 9) suggested that a single major gene effect may be responsible for the exploratory activity of mice, even in the presence of other genes that may contribute to the genetic variance of this trait. Since the congenic line H (w26) (a line differing from C57BL/6By itself by only an introduced chromosomal segment including a BALB/cBy allele at the H (w26) locus) displayed the same SDP and was characterized by low exploratory activity (like the BALB/cBy strain), proof of locus identity was obtained. The symbol *Exa* was suggested to designate the locus, linked to H (26) in Chromosome 4 for basal exploratory activity, with *Exa*^h to designate the allele determining the high level, and *Exa*^l the allele determining the low level of activity (Oliverio, Eleftheriou & Bailey, 1973). Similarly, it was possible to ascribe to a single gene a major effect on a complex behaviour trait such as active avoidance learning. The symbol Aal (active avoidance learning) was used to designate its locus linked to H(w56) on Chromosome 9 (LG11) (Oliverio, Eleftheriou & Bailey, 1973). The isolation of the genes controlling these behavioural units in extant congenic lines now allows for more definitive studies on many behavioral phenomena and their physiological and biochemical phases.

A large number of experiments has indicated that many behavioural differences in humans are determined to a large extent genetically. A comprehensive review of more

Figure 9. Distribution of mean activity (mean number of crossings in toggle-floor box) in the backcross $B6CF_1 \times BALB/cBy$ and in the parent strains $BALB/cBy$ and $C57BL/6By$. Each point represents the performance of a different mouse, (Oliverio, Eleftheriou & Bailey, 1973).



than 50 different studies carried out by Erlenmeyer-Kimling & Jarvik (1963) indicate that intra-group resemblance in behavioural and "intellectual" activities increases in proportion to the degree of genetic relationships. The correlations between couples of unrelated persons were close to zero while reaching the 50 % value for parent-child and a level of nearly 90 % for twins raised together. Similarly, different types of mental diseases are also genetically conditioned. Studies conducted by Kety, Rosenthal, Wender & Schlusinger (1968) and Heston (1970) show that schizophrenic and schizoid syndromes are mostly connected with inborn factors. Recently, Fieve and his associates at the Columbia University by using colour blindness and XgA blood group as genetic markers were able to demonstrate linkage between these two genes, which are on the X chromosome, and one exerting a major role in susceptibility to manic depressive illness. These are just a few examples showing that there are various genetic mechanisms which are responsible for the observed individual differences in behaviour and for many psychopathological patterns. It is rather difficult to discover in humans the properties of the nervous system which are the grounds for these differences, while a comparative study and a psychogenetic analysis may represent a powerful method. The comparative approach offers useful models for the study of different behavioural patterns: the affectional and social behaviour of monkeys and apes and the effects of postnatal experience are just a few examples of the kind of analysis that can be conducted at the animal level. It has been suggested for a long time that there is a clear distinction between the mechanisms of animal intelligence, which is mostly a "concrete" intelligence, and those of human intelligence, which is mostly symbolic. In addition, cultural evolution should differentiate Man from animals. We know today that concrete, "motor" intelligence characterizes the ontogenetic development of Man (Piaget, 1964) and that symbolic processes and cultural evolution are also evident in animal societies (Washburn & Shirek, 1967;

Mainardi & Pasquali, 1968). The psychogenetic approach has clearly shown that there are differences in the abilities of mice, rats, monkeys and men which are the products of evolutionary adaptive processes and that the analytical tools are available for their study. Knowledge of the genetic systems that underlie the differences between individual mice or strains, of their mode of inheritance and of the gene or polygenes involved is a necessary background for understanding the neurophysiological and biochemical foundations of human behavioural differences. As for other fields in the biological sciences, the study of the individual differences and of the evolutionary aspects of behaviour, based so far on a comparative approach, will progress and benefit from a genetic analysis.

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J. Lessertisseur

*Laboratoire d'Anatomie
comparée du Muséum national
d'Histoire naturelle, Paris*

J.-P. Nakache

*Centre de Calcul et de Statistique
du CHU Pitié-Salpêtrière, Paris*

N. Petit-Maire

*Laboratoire de Géologie du
Quaternaire C.N.R.S. 92-Bellevue,
Paris, France*

Application of Principal Component Analysis Using the Chi-Square Metric ("Analyse Factorielle des Correspondances") to the Study of Cranial Characters in Primates

Two types of multivariate analysis of cranial metrical data have been tried for the whole Primate Order (Hominoidea excluded). The Prosimian heterogeneous group has been analysed in greater detail. Principal component analysis using the Chi-square metric for 16 parameters resulted in good differentiation of subgroups, often down to generic level. Discriminant analysis pointed out the major importance of the opposition cranium-masticatory apparatus, in the whole order and at all taxonomical levels, together with the high weight of basal width discriminating power for comparison of Primate skulls shape. Thus, it seems legitimate to use such methods in our future research for locating fossil specimens with a limited number of measurements.

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1. Introduction

This paper is part of the Primates studies already published by one of us (N. P. M.), the aim of which is to provide palaeontologists with a synthetic view of modern Primate skull variation (adult and growth data). In our mind, phylogenetic interpretations can no longer be made without a precise knowledge of present and past polymorphism. Moreover, elimination of unnecessary (correlated or insignificant) measurements is absolutely necessary; computers provide us with the means to do so objectively for all Primates (as it was done for human crania only, at the infra-specific level, by W. W. Howells). We tried here to determine which type of analysis could be securely applied to very heterogeneous inter-generic data.

In numerical taxonomy (whatever criticisms have been levelled at the principle) numerous methods have already been used, but multivariate analysis, in its different forms, is the most satisfactory, because of both the scope and precision of the data it may consider.

Such a taxonomy, when applied to Primates, would require the consideration of all the significant characteristics of the group: anatomical and biometrical traits, and also biochemical, caryological, serological, embryological, and even behavioural characteristics. Such research, although our ultimate aim, could not be done yet and, as a first step, we decided instead to reverse the problem and try a different method: in a given group (Primates), studied under a given angle which we suppose to have a systematic value (cranial size and shape), will the results of such a factorial analysis fit the classical data for this group?

Our aim may seem useless, since the material work involved does not give any sure promise of scientific benefit. However, we must be aware of two points: (1) comparing the results of classical taxonomy with those obtained through numerical taxonomy is useful, since it always brings new problems to light; (2) the aims and the advantages of

both methods are clearly different, although their results, far from excluding each other, complement each other. For instance, when seeking to locate a fossil specimen for which, possibly, only a few measurements have been taken, the risk of error will be minimized if the statistical re-partition of the whole group data is known. The probability of fitting the specimen into a particular subset of the group is then calculated with great accuracy. The ultimate aim of the preliminary research we present here, fits in such a scope and is but the first step in a much wider study.

Since cranial study was chosen first, a preliminary criticism of the parameters which were employed seemed necessary: we firstly eliminated the characteristics which proved useless for Primate discrimination in our earlier studies and those of other primatologists: evident correlations or functional connections which could have biased the interpretations. (For instance, out of the two cranial heights available—porio-bregmatic and basio-bregmatic heights—we chose the latter, which describes with greater accuracy the total morphological pattern.) On the other hand, we kept both basal width measurements—bi-auricular and bi-stylo-mastoid—since we were considering the whole order of Primates, not only the Hominoidea: the highly significant differential morphology in the mastoid region had to be evaluated properly, in such a heterogeneous set. The results obtained proved the correctness of such an estimation for discriminant value. Unfortunately, a further elimination of parameters was necessary due to the lack of well preserved specimens for certain morphological zones.

Thus, the reduced number of parameters used in this research—although contrary to the normal practice in modern systematics—was carefully considered. In any case, we were testing a method here and our ultimate purpose was to integrate more reasonable and diversified parameters related to total Primate morphological variation.

As for the problem of correlations, the method itself indicates the remaining metric organically-related connections between the elements of the organized set considered here, i.e. cranium (in which individual and specific variation of characters always depend functionally more or less acutely one upon the other).

The advantage of the principal component analysis, in this case, is to give a simultaneous representation of individual repartition and of the parameters' role. The proximity of the very parameters is greatest when correlations are highest: which is very useful for interpretation.

2. Multivariate Analysis

(a) *Method*

Multivariate statistical analysis is used when one is dealing with a great amount of data contained in a rectangular array where the lines represent the set of "individuals" (in our case, the skulls) and the columns, the set of parameters measured on the individuals.

Multivariate analysis allows one to take into account all the measurements defining the individuals and aims to get interesting information from the set of correlations which can exist between them all. The set of individuals is referred to a p -dimensional space R^p generated by the p axes defining the p parameters: a skull is then represented in this R^p space, by a point or element, the components of which are its p measurements. All

the skulls constitute in this space a "cloud" of points. The problem is to define the *form* and the *dispersion* of this cloud around its "gravity centre." This work is done by using factorial analysis.

Factorial analysis

Factorial analysis is a multivariate technique, the purpose of which is to define a new reference system for the points, their axes being the principal directions of the cloud. Thus, we use in the interpretation the only axis explaining a significant part of this dispersion, thereby reducing the dimension of the new reference system. The factorial axis of this new reference system summarizes the set of parameters of the study. Factorial analysis is based upon a distance notion between the individual points and is used to define the dispersion of the cloud.

Principal component analysis, as a factorial analysis, is based on the usual Euclidian distance. This analysis is used particularly to describe an homogeneous set of data, i.e. data measured in the same unit (which is the case for our data). Nevertheless, principal component analysis is inconvenient: it gives great importance to the "size factor." Since our research aims more to seek for "shape factors," size, for us, may be considered as a "parasite" effect. In order to avoid this inconvenience, we used another distance method (chi-square distance) for defining the proximities between the individual points of the cloud.

Chi-square distance

Due to J. P. Benzecri, this distance suits the analysis of data expressed in positive occurring numbers. Practically, it seems to fit the computing of homogeneous data like those of our study.

This distance is calculated from the conditional frequencies (see Appendix) which allow a comparison between the individual profiles. On the other hand, by not giving too important a part to one parameter, we introduce a weighing factor (weight of the parameter) into the quantities which constitute this distance (see Appendix).

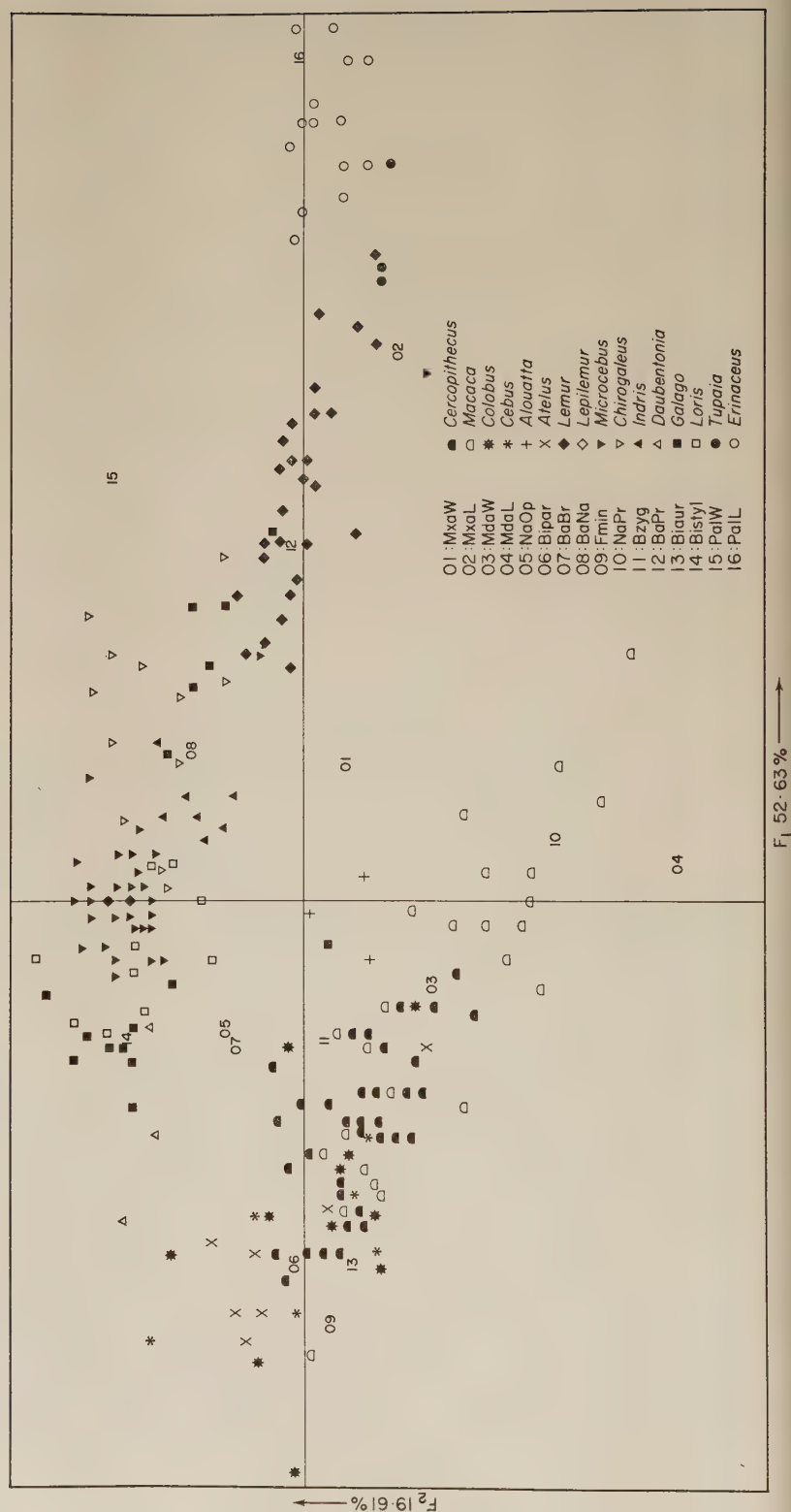
The factorial analysis based on the chi-square distance is called, "*Analyse factorielle des Correspondances*." In this analysis, the sets individuals and parameters play a symmetrical part and the data are transformed into frequencies which do not change the information contained in the data.

The properties of the chi-square distance lead to a rigorous *simultaneous graphical representation of the two sets*, individuals and parameters, in a sub-space of restricted dimension respecting the distances between the elements of the two sets. In this graphical representation, the proximity between an individual-point and a parameter-point has a precise meaning: an individual-point is located near the elements of the parameter set to which it is the best associated and *vice versa*. Furthermore, two individual points having the same profile are indistinguishable on the graph. In the case when the points location is not changed by projection on the graph, the smaller the distance between two parameter points, the greater the correlation between these two parameters.

It is thus possible to classify the individuals, to characterize the classes obtained and to give an interpretation of the significant factorial axis. This simultaneous graphical

Figure 1. "Analyse factorielle des Correspondances" for 213 adult primate crania (Hominoidea excluded) and 16 parameters. On this figure and the following ones, the individuals-points are represented by conventional signs corresponding to genera and the parameters-points are represented by numbers. (Maxillar anterior arcade width, Mandibular anterior arcade length, Mandibular anterior arcade width, Maxillar anterior arcade length, Nasion-Opisthocranion, Biparietal width, Basion-Bregma, Basion-Nasion, Minimal frontal width, Nasion-Prosthion, Bizygomatic width, Basion-Prosthion, Biauricular width, Bistylomastoide width, Palate width, Palate length.)

In every case, the plane chosen is the one given by the first two axes ($F_1: F_2$).



representation is possible only by using the chi-square distance, i.e. only through an "analyse factorielle des correspondances" and not, for example, through a classical principal component analysis.

(b) Applications

For a first trial, we applied this method successively to the whole of primate order (*Hominoidea* excluded at first, since our sample was not sufficient for all measurements), then only to the Prosimians, considered as the most heterogeneous group. Several successive steps have been taken, summed up in Figures 1, 2 and 3. As a term for comparison, *Insectivora* (*Tupaia* and *Erinaceus*) have been located upon the graphs, as they had already been in the growth research published by one of us (N. P. M. 1970-71).

Figure 1

Figure 1 gives the results of an "Analyse Factorielle des Correspondances" for 213 Primate crania and 16 parameters: the measurements have been mostly chosen among those registered and computed by one of us (N. P. M. 1966-1971) for 1842 Primate crania from all the zoological families in the order. The measurements of some new specimens (Prosimians) have been added on Figure 2(b).

The measurements are few, but we had to limit ourselves to those accounting for *homologous points* and to exclude, of course, evident correlations (although maxillar and mandible measurements correlate sharply and palatal length is a part of facial length, they have been kept for ulterior fossil location).

The first two axes of the graph account for more than 72 % of the observed variation. We shall not consider the other ones. Clearly, Primates split into two major discontinuous

Table 1 **Sample**

Genera		Parameters	
<i>Cercopithecus</i>	38		
<i>Macaca</i>	28	Width of superior dental arcade, behind the P_4	1
<i>Colobus</i>	3	Corresponding mesio-distal length	2
<i>Semnopithecus</i>	8	Width of inferior dental arcade, behind the P_4	3
<i>Alouatta</i>	3	Corresponding mesio-distal length	4
<i>Ateles</i>	5	Cranial length (Nasion-Opisthocranium)	5
<i>Lagothrix</i>	2	Cranial width (Bi-parietale)	6
<i>Cebus</i>	6	Cranial height (Basion-Bregma)	7
<i>Lemur</i>	28	Basal length (Basion-Nasion)	8
<i>Microcebus</i>	12	Minimal frontal width	9
<i>Chirogaleus</i>	27	Face height (Nasion-Prosthion)	10
<i>Phaner</i>	2	Face width (Bi-zygomatic)	11
<i>Daubentonia</i>	3	Face length (Basion-Prosthion)	12
<i>Propithecus, Indri</i>	9	Base width (Bi-auriculare)	13
<i>Galago</i>	16	Base width (Bi-stylomastoid)	14
<i>Loris, Nycticebus</i>	4	Palate width (method N.P.M. 1961)	15
<i>Perodicticus</i>	6	Palate length (method N.P.M. 1961)	16
<i>Tupaia</i>	3		
<i>Erinaceus</i>	14		
	215		

groups. Insectivora isolate at one end of the graph, but are not clearly separated from Prosimians, while Simians are isolated from all the others.

The only exception for this rule is the location obtained for *Daubentonia* (closer to Simians than to other Prosimians), which seems perfectly logical, when one considers its cranial morphology.

Each of these axes may be studied with greater precision.

The F_1 axis, responsible for the major dispersion, accounts for 52.36% of variation. The importance of size, reduced by the method here employed, is rather small. Its bipolarity displays from frontal width to palate length, and puts into evidence the best differentiating parameters in Primates, corresponding to the opposite phenomena of cerebralization and facialization, in spite of the absence of *Hominoidea*. The location of some other parameters towards the polar ends confirms this view: on one side, frontal width, biparietal width, basal width; on the other, palate length, length of anterior dental arcade and face length.

Along this first axis, we find successively, in projection and from left to right (i.e. cerebralization decreasing): *Platyrrhini* (*Cebus*) and *Colobinae* (the least affected by facialization), then *Cercopithecidae* (*Macaca*, *Cercopithecus*), with a wide range of variation and overlapping which may be due to heterogeneity in species and to sexual dimorphism.

In projection on the F_1 axis, the Prosimian variation overlaps widely the Simian one; thus, a few Prosimians (*Daubentonia* and some of *Galago*) appear to be less "facialized" than most *Cercopithecidae*. However, as a whole, the sub-order extends far on the right side of the graph with no hiatus in repartition and constant overlapping of the successive groups variations: *Lorisidae*, *Cheirogaleinae*, *Indriinae*, some *Galago* (see below) and, last of all actual Primates, *Lemur*, the most extreme specimens of which form a continuum with the *Tupaiaidae*. Extreme facial development culminates, logically, in *Erinaceus*, isolated, but without clear rupture in the continuum, on the right pole of the graph.

The F_2 axis accounts for 19.51% of total Primate variation (*Hominoidea* excluded). Its interpretation is more difficult: its inferior pole is clearly characterized by two facial parameters (anterior length of dental arcade and face height) around which all *Macaca* are located, due to the extreme specialization of their Incisive and Canine masticatory apparatus. On the opposite pole appears palate width, but also central basal width (bistylomastoid) and most of the Prosimians gravitate around it. However, these parameters are located too close to the origin to have a really clear significance.

To sum up the whole graph, a single real rupture appears in the continuity of Primate forms: the one showing clearly between the Prosimians and Simians; no morphological intermediate appears (maybe *Daubentonia*?). This result fits with the antiquity of phylogenetic separation between groups which is generally admitted. On the contrary, the relative homogeneity and all the overlapping variation ranges within each sub-order are probably a result of the more numerous common genetic characters involved in closer species (especially in *Catarrhini* and *Platyrrhini*).

The intermediate location of *Tupaia* between Primates and Insectivora confirms the hypothesis of a more or less similar Primate ancestral form.

The sub-division of *Galago* into two well separated groups is certainly partly due to the important size differences existing between the species under consideration (*G. senegalensis*, *G. crassicaudatus* and *G. demidovii*), but differences in shape also appear in cranio-facial relations. Finer interpretation of this research will allow us, in the future, to clear up this problem.

Figure 2(a)

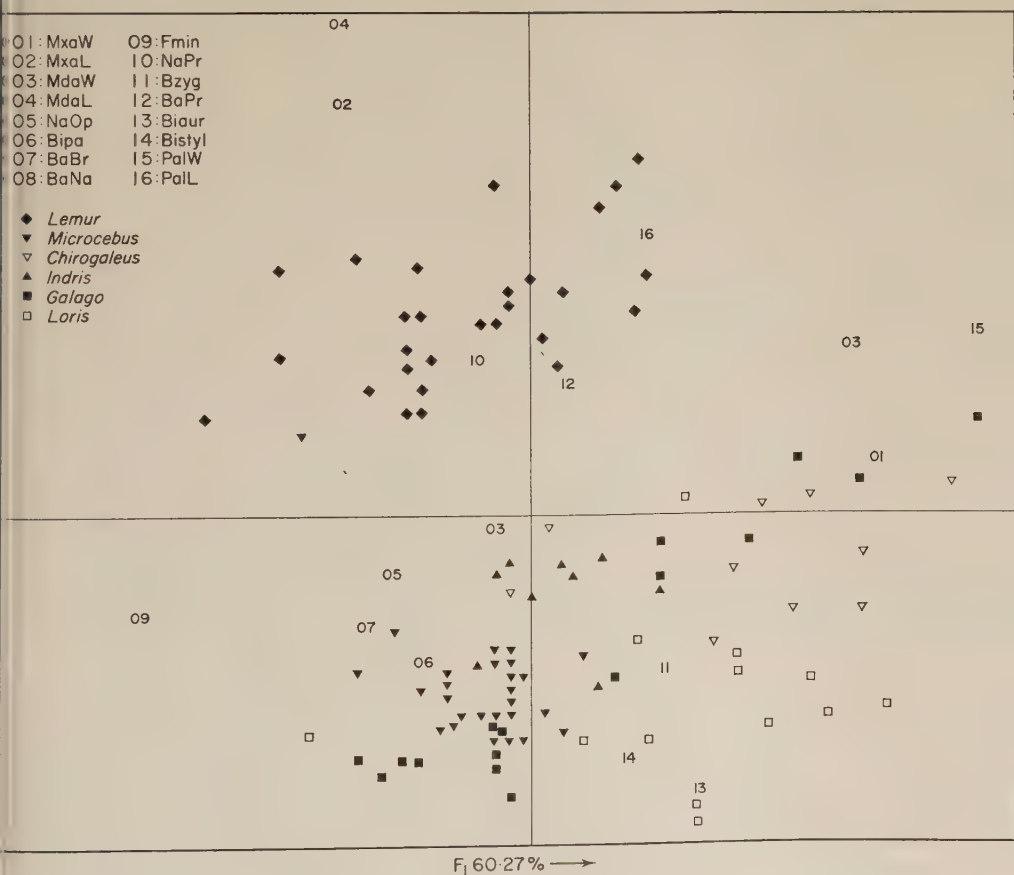
Looking for a finer taxonomical level, we have, for the moment, tried to split the more heterogeneous of our groups—Prosimians—according to the same analysis principles. Figure 2(a) shows the results for 106 individuals and the same 16 parameters as considered in Figure 1.

A neat splitting appears clearly between two major groups: toward the upper pole, the *Lemuridae*, toward the lower pole, all the other Prosimians (once again, *Daubentonia* seems apart from both groups, although we can only consider three individuals).

Axis F_1 accounts for 60.27% of total Prosimian variation. The parameters involved are, on one side, frontal width and on the other, anterior arcade or palate width. Thus, the same opposite factors already playing a part in the total Primate differentiation keep their major part within the isolated Prosimians.

The two well separated *Galago* groups we noted before, appear still more clearly here. This first axis does not distinguish clearly the classical groups, the projections of which overlap quite noticeably.

Figure 2(a). "Analyse factorielle des Correspondances" for the whole set of our 106 adult *Lemuroidea* crania and 16 parameters.



Axis F_2 accounts for 11.61 % of variation. Polar parameters appear clearly, anterior arcade length being opposed to central basal width (as already seen in Figure 1). Total basal width is less significant, undoubtedly because of the auditory process variation involved in its structure.

This axis is the one which isolates *Lemur* from the rest of our sample. It also allows the bipartition of the two *Galago* groups.

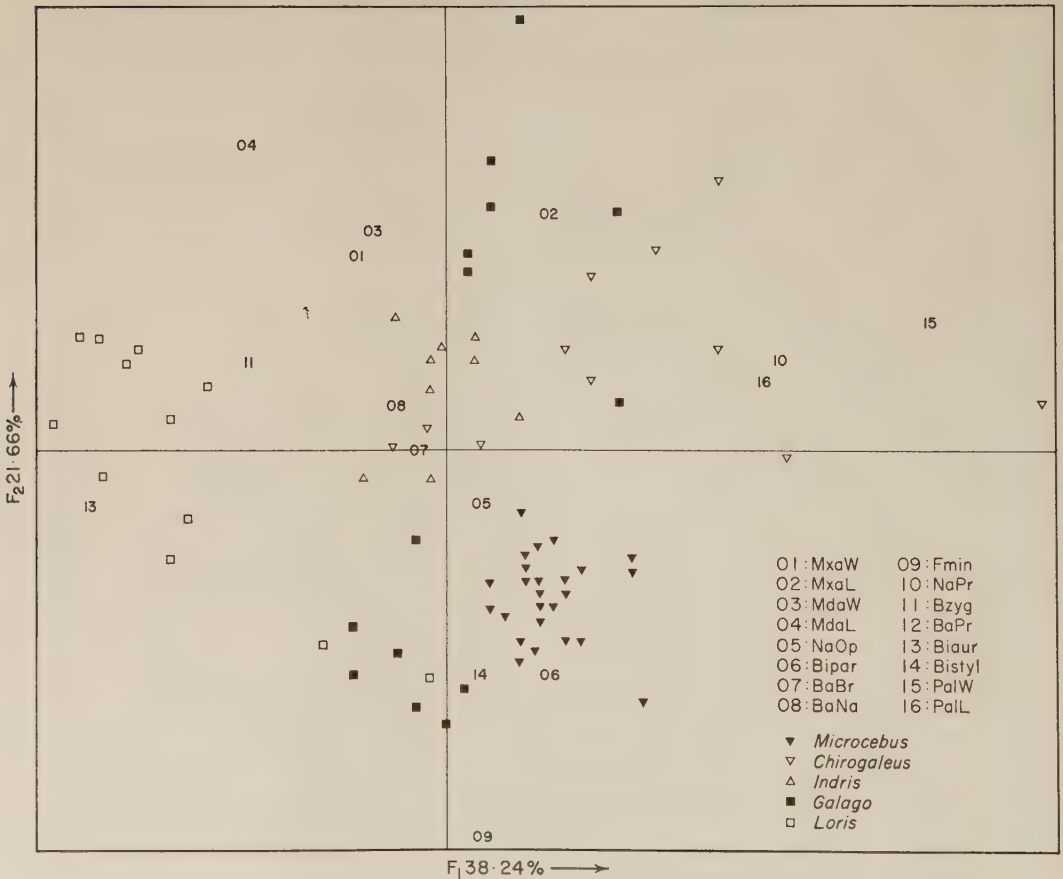
Figure 3

Since the preceding analysis (Figure 2(a)) isolated *Daubentonia* and *Lemur* from the other Prosimians, we thought it worth establishing the relations existing between the rest of our sample. This new splitting could be worked on for the same 16 parameters and 74 individuals.

The first two axes account for about 60 % of variation.

F_1 (38.24 %) separates the species with a high face and a well developed palate and those (*Loris*, *Perodicticus*) with a wide total base.

Figure 3. "Analyse factorielle des Correspondances" for part of the *Lemuroidea* set (*Lemur* and *Daubentonia* excluded): 74 adult crania, 16 parameters.



F_2 (21.66%) is still characterized by cranio-facial bipolarity: extreme parameters are again frontal width on one side and anterior arcade length on the other. In spite of the sometimes very important overlapping of species variation, some interesting facts show up: the median location of *Indriinae* and *Lorisinae*, the clear differentiation appearing between the two *Cheirogaleinae* genera: *Chirogaleus* and *Microcebus*, the extreme division of *Galago*, the smallest species being placed near *Microcebus* and the largest one near *Chirogaleus*.

Thus, the successive splitting of the initial total group (Prosimians, then Prosimians minus *Lemuridae* and *Daubentonidae*) has isolated with satisfactory precision the various forms belonging to a rather confused whole. However, the successive eliminations do not always coincide with the importance given to these groups in classical systems. We are not surprised at the isolation of *Daubentonia*; on the contrary we could not expect such a drastic separation of *Lemurinae* at first splitting. The clear differentiation of *Chirogaleus* and *Microcebus*, and the constant bipartition of *Galaginae*, not only for size factors, were not to be expected either.

One must not forget, however, that the method used in this research cannot be considered *a priori* as a significant guide from which to draw phylogenetical conclusions. As for taxonomy, it can only point out metrical similarities or differences, the meaning of which must then be discussed in detail. This objection is a well-known one applied to numerical taxonomy studies.

Figure 2(b)

The process of successive elimination which we applied to the best characterized group in our sample, in order to get a progressively finer analysis, can be applied to the very parameters, and thus account for the importance of each one of them in the repartition of the whole.

At every level in our preceding analysis, we noticed the high significance (which is logical) of the opposition muzzle-cerebral cranium. We thus wondered what would happen if we eliminated one of these factors, for instance the measurements of the dental anterior arcade, which always account for a great part of the total dispersion and are located in a polar position.

To be compared with Figure 2(a), discussed above, we prepared Figure 2(b) out of 112 measurements (the 4 measurements of superior and inferior arcade being taken out) and 127 skulls from the Prosimian group.

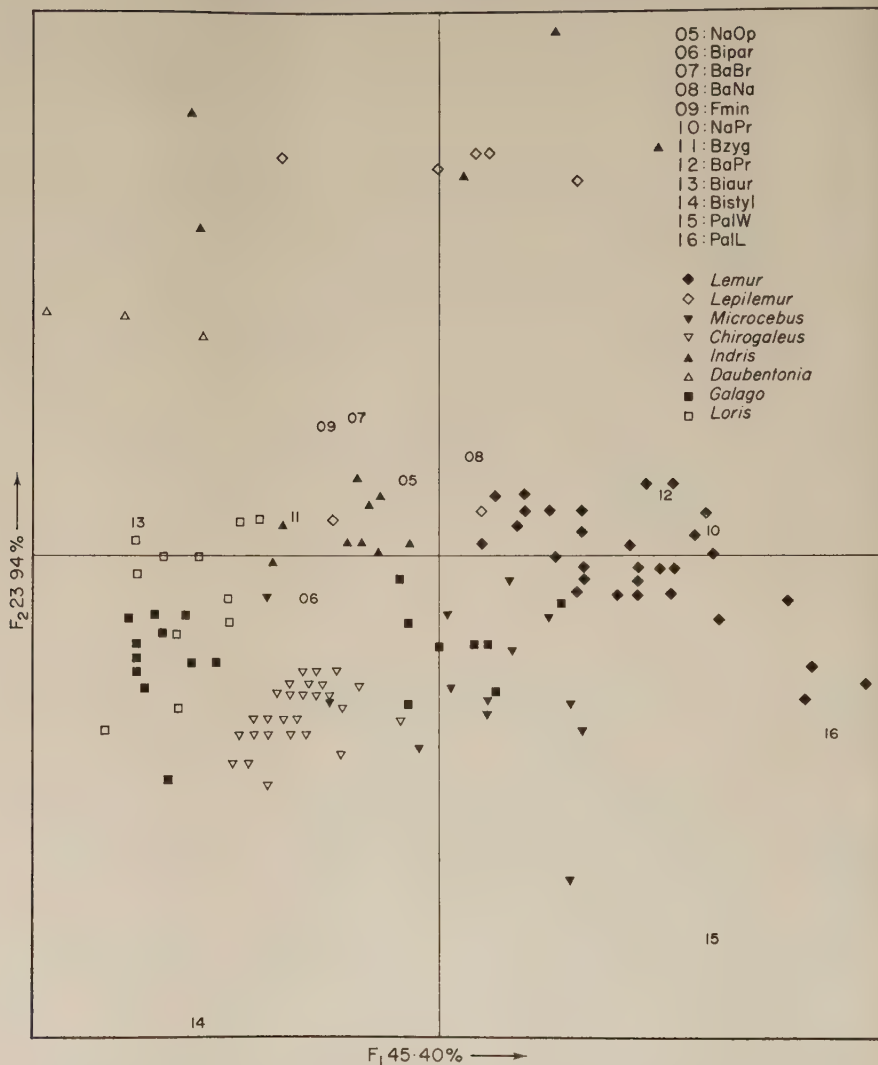
As a logical result, we first notice that the principal zoological groups are less separated than in Figure 2(a) (with arcade).

Axis F_1 (inertia = 45.40%) does not completely isolate the *Lemur* group, although *Cheirogaleinae* (*Microcebus* and *Chirogaleus*) remain apart, with always the same separation of the two genera.

Table 2 **Sample**

<i>Lemur</i>	30	<i>Microcebus</i>	12
<i>Lepilemur</i>	6	<i>Chirogaleus</i>	28
<i>Hapalemur</i>	1	<i>Phaner</i>	1
<i>Indris, Propithecus</i>	14	<i>Daubentonia</i>	3
<i>Galago</i>	20	<i>Loris</i>	4
<i>Perodicticus</i>	8		

Figure 2(b). "Analyse factorielle des Correspondances" for 217 adult crania and 12 parameters (dental arcade measurements excluded) on the whole set of the *Lemuroidea* group. [cf. Figure 2(a)].



The anterior masticatory apparatus differences not being taken into consideration, another facial parameter takes their place (palate measurements opposing now basal width), which was to be expected. It confirms the research published by one of us (N. P. M.) on the major importance of the anterior arcade measurements in Primate discrimination (and not only in human phylogeny). They are the characters with the best discriminating power, since the dental specialization in most Primates concerns the Incisives + Canine + Premolars stock. Palatal dimensions may, of course, take their place, but are less precise.

Axis F_2 (inertia = 23.94%) is difficult to interpret. On the left side, a number of skulls have an "abnormal" position and we used, to find an explanation, the discriminant analysis which will be described later.

The deceptive results obtained with Figure 2(b) show how difficult and dangerous it may be to classify a fossil fragmentary specimen in which the main discriminating parameters fail to appear, the muzzle zone for instance, which it is not easy to deduce from the upper-cranial part, on account of mosaicism.

3. Discriminant Analysis

(a) Method

Linear discriminant analysis. Factorial analysis is used to describe an array of data displaying clusters, if they are any, and their characterization. On the contrary, discriminant analysis is applied to a set of "individuals" described through a certain number of parameters and divided into two or several *a priori* defined groups. In this case, the aim is the determination, among the parameters, of a hierarchical set of parameters of reduced dimension allowing the best discrimination or differentiation between the clusters. This is the first step in discriminant analysis, called descriptive step.

This subset of discriminant parameters results in a decision function or discriminant function, used for the problem of location which is the essential part of discriminant analysis: one gets a new specimen and supposes that it belongs to one among the definite groups. He wishes then to determine which, with a minimal risk of misclassification. This second part of discriminant analysis is the decisional step.

To define this subset of hierarchical discriminant parameters (parameters with a significant power of discrimination) we use a stepwise procedure, finding, at first, the best discriminant parameter, then the two best ones, then the three best ones etc. The step procedure test is related to the percentage of well classified individuals.

When one has three or more groups, a factorial discriminant analysis can then be applied to define the principal directions of the "mean points cloud" for the different groups. For three groups, the analysis leads to their graphical representation on the unique factorial discriminant plane. This plane divides, at best, the mean points of the considered groups.

In this paper, we only used the first step of the analysis.

(b) Application (Figure 4)

To verify the value of this method for our sample, we computed a step by step discriminant analysis of the whole Prosimian suborder, separating it arbitrarily into three groups of approximately same numerical importance (as required by the method) but zoologically heterogenous:

Group 1 $n = 37$: *Lemur*, *Lepilemur*, *Hapalemur* (*Lemurinae*)

Group 2 $n = 41$: *Chirogaleus*, *Microcebus*, *Phaner* (*Chirogaleinae*)

Group 3 $n = 49$: the heterogeneous group formed by the other Prosimians (*Indriinae*, *Daubentonia*, *Lorisidae*).

Figure 4. Discriminant analysis for 12 parameters and 127 adult *Lemuroidea* crania, parted arbitrarily into three groups; 1 *Lemurinae*, 2 *Chirogaleinae*, 3 other *Lemuroidea*. ● = the gravity centre of the whole group; * = the gravity centres of each of the 3 subgroups.



4. Conclusions

We never meant to use such numerical analysis to infer systematics or phylogeny in the considered groups. A criticism of numerical taxonomy (very widely used since Sokal & Sneath first researched in 1957) is thus irrelevant. We are perfectly conscious that a classification based upon mere morphological proximities could have no value since it does not consider actual evolutive phenomena: mosaïc processes, differential evolutive rates for the varied characteristics and differential evolutive rates in the varied lineages considered. Thus, a species related morphologically to one or several others for a certain number of characteristics may be zoologically much further from them than apparently closer forms—since the rate of evolution of the latter may have been higher for these precise characteristics.

No numerical method can tell whether a morphological relationship is due to parentage or convergence—if no palaeontological data are available for control.

Our aim was thus a modest one: to determine whether principal component analysis could be of some help in clarifying morphological differences in Primate crania, and thus be used in later studies for setting a sample (a fossil one for instance) securely enough within a morphological group—using a small number of fundamental parameters—and thus eliminating a great number of useless measurements, saving time and gaining security.

Methods

Two points have to be discussed: first, how secure was the multivariate analysis we used, as far as the morphological and taxonomic significance of a wide heterogeneous zoological group is concerned; second, how secure is the analysis performed for judging of parameters discriminant value.

Thanks to our first multivariate analysis (Figures 1–3), we could separate with accuracy the classically admitted Primate groups (with a few interesting exceptions which will be considered in a further paper). The importance of the discrimination also does not always correspond to the taxonomic level (superfamily down to species) generally attributed to the individuals here considered. In this respect, let us point out once more the purely morphological significance of such a numerical analysis, above all when only present species are considered. The theoretical importance of a datum does not fit exactly and *a priori* its apparent phenotypical importance, for all the genetical reasons one knows well. (A principal component's analysis on such data as ours has made size responsible for more than 89% of total variation in the whole Primate sample!) One should not feel surprised if, for instance, the two *Galago* subgroups look more widely separated on our Figures than the two essential anatomical units: *Lemuridae* and *Lorisidae*.

However, our analysis seems fit to classify, with a minimal probability of inaccuracy and a minimal number of measurements, any Primate skull (belonging to the families here considered).

Discriminant analysis results are, in our sense, still far more interesting, since they provide us with the possibility of choosing objectively, for any Primate study, the more significant measurements, not bothering with the others. (The multiple contradictory researches and the impossibility of working out meaningful synthesis are thus eliminated.) We are glad that the methods applied by W. W. Howells to analysis of recent human crania can be successfully applied to a whole zoological order, which was long doubted.

The confirmation of basal measurements importance in Primate studies (together with anterior masticatory apparatus and cranial anterior frontal width importance, as in the upper Hominid and Pongid species) is of the highest importance for comparative anatomy and palaeontology studies.

Our next step will be the completion of these analyses with Hominoidea specimens, then locating fossil specimens on the graphs. Thus, computing data will certainly—in spite of the inherent danger—bring a new life into zoological studies. Another aim of ours is to use this type of analysis for interpretation of the more significant set of Primate characters we have listed at the beginning of this paper. Of course, one will not be able to use such a matrix to locate fossil specimens, but a more secure approach to phylogenetical hypothesis will thus be provided.

Appendix

Summary of technical method of "Analyse factorielle des correspondances"

Observations array:

$X = (p, n)$ matrix with x_{ij} as general term; $i = 1, 2, \dots, n$

$T = (n, p)$ matrix with x_{ij} as general term; $j = 1, 2, \dots, p$

$$X = T'$$

Relative frequencies:

$$P_{ij} = x_{ij} / \sum_{i=1}^n \sum_{j=1}^p x_{ij},$$

$$P_{i.} = \sum_{j=1}^p P_{ij},$$

$$P_{.j} = \sum_{i=1}^n P_{ij}.$$

Analysis of n individuals in the R^p space

Observations array:

$$X = \begin{bmatrix} x_{11} & \cdots & x_{i1} & \cdots & x_{n1} \\ x_{1j} & \cdots & x_{ij} & \cdots & x_{nj} \\ x_{1p} & \cdots & x_{ip} & \cdots & x_{np} \end{bmatrix}.$$

"Cloud" $N_I = \{n \text{ individual-points } \mathbf{x}_i \text{ weighted by } P_{i.}\}$

$$x_{ik} = \frac{P_{ik}}{P_{i.} \sqrt{P_{.k}}} \quad (k = 1, 2, \dots, p).$$

Distance between two individual-points "i" and "i'" of N_I

$$d_{i,i'}^2 = \sum_{j=1}^p \left(\frac{P_{ij}}{P_{i.} \sqrt{P_{.j}}} - \frac{P_{i'j}}{P_{i'.} \sqrt{P_{.j}}} \right)^2.$$

Quadratic form associated to d^2 : $M = I$

$I = (p, p)$ unity matrix.

Variance-covariance matrix of $X = S_{JJ}$
(p, p)

general term:

$$s_{jj'} = \sum_{i=1}^n \frac{P_{ij} \cdot P_{i'j'}}{P_{i.} \sqrt{P_{.j}} \sqrt{P_{.j'}}}.$$

Characteristic equations of S_{JJ} and S_{II}

$$S_{JJ} \mathbf{u}_r = \lambda_r \mathbf{u}_r$$

where $\mathbf{u}_r' \cdot \mathbf{u}_r = 1$.

Analysis of p parameters in the R^n space

Observations array:

$$T = \begin{bmatrix} x_{11} & \cdots & x_{1j} & \cdots & x_{1p} \\ x_{i1} & \cdots & x_{ij} & \cdots & x_{ip} \\ x_{n1} & \cdots & x_{nj} & \cdots & x_{np} \end{bmatrix}.$$

"Cloud" $N_J = \{p \text{ parameter-points } \mathbf{x}_j \text{ weighted by } P_{.j}\}$

$$x_{lj} = \frac{P_{lj}}{P_{.j} \sqrt{P_{.j}}} \quad (l = 1, 2, \dots, n).$$

Distance between two parameter-points "j" and "j'" of N_J

$$d^2(j, j') = \sum_{i=1}^n \left(\frac{P_{ij}}{P_{.j} \sqrt{P_{.j}}} - \frac{P_{i'j'}}{P_{.j'} \sqrt{P_{.j'}}} \right)^2.$$

Quadratic form associated to d^2 : $M = I$

$I = (n, n)$ unity matrix.

Variance-covariance matrix of $T = S_{II}(n, n)$

general term:

$$z_{ii'} = \sum_{j=1}^p \frac{P_{ij} \cdot P_{i'j'}}{P_{.j} \sqrt{P_{.j}} \sqrt{P_{.j'}}}.$$

$$S_{II} \mathbf{w}_r = \rho_r \mathbf{w}_r$$

where $\mathbf{w}_r' \cdot \mathbf{w}_r = 1$.

Comparison of S_{JJ} and S_{II} eigen vectors and eigen values

Y is a (pn) matrix with general term $y_{ij} = \frac{P_{ij}}{\sqrt{P_{i.}}\sqrt{P_{.j}}}$ $i = 1, 2, \dots, n; j = 1, 2, \dots, p$

$$\begin{array}{c|c} Y = X \cdot D\sqrt{P_{i.}} & Y' = TD\sqrt{P_{.j}} \\ \hline (p, n) & (n, p) \end{array}$$

where $D\sqrt{P_{i.}}$ and $D\sqrt{P_{.j}}$ are respectively diagonal matrix (n, n) and (p, p) with $\sqrt{P_{i.}}$ and $\sqrt{P_{.j}}$ as general term

$$\begin{array}{c|c} S_{JJ} = YY' & S_{II} = Y'Y \\ \hline YY'\mathbf{u}_r = \lambda_r\mathbf{u}_r & Y'Y\mathbf{w}_r = \rho_r\mathbf{w}_r \\ Y'Y(Y'\mathbf{u}_r) = \lambda_r(Y'\mathbf{u}_r) & \\ \mathbf{w}_r = Y'\mathbf{u}_r & \\ \mathbf{w}'_r\mathbf{w}_r = \lambda_r & \end{array}$$

$$\boxed{\mathbf{w}_r = \frac{1}{\sqrt{\lambda_r}} Y'\mathbf{u}_r \text{ with } \mathbf{w}'_r\mathbf{w}_r = 1.}$$

$$\begin{array}{l} \rho_r = \lambda_r \ (r = 1, 2, \dots, p) \\ \rho_r = 0 \ (r = p + 1, \dots, n) \end{array}$$

Individual-points components on factorial axis $\Delta_{\mathbf{u}_r}$

$$\begin{array}{l} \mathbf{f}_r = X' \cdot \mathbf{u}_r \\ (n, 1)(n, p)(p, 1). \end{array}$$

Relation between $\mathbf{f}_r$ and $\mathbf{w}_r$

$$\mathbf{f}_r = \sqrt{\lambda_r} \cdot D_{1/\sqrt{P_{i.}}} \cdot \mathbf{w}_r$$

symmetrically

Parameter-points components on factorial axis $\Delta_{\mathbf{w}_r}$

$$\begin{array}{l} \mathbf{g}_r = T'\mathbf{w}_r \\ (p, 1)(p, n)(n, 1). \end{array}$$

Relation between $\mathbf{g}_r$ and $\mathbf{u}_r$

$$\mathbf{g}_r = \sqrt{\lambda_r} D_{1/\sqrt{P_{.j}}} \cdot \mathbf{u}_r$$

Relation between $\mathbf{f}_r$ and $\mathbf{g}_r$

$$\mathbf{u}_r = \frac{1}{\sqrt{\lambda_r}} D\sqrt{P_{.j}}\mathbf{g}_r$$

$$\text{then } \mathbf{f}_r = \frac{1}{\sqrt{\lambda_r}} X' D\sqrt{P_{.j}}\mathbf{g}_r$$

$$\text{and symmetrically } \mathbf{g}_r = \frac{1}{\sqrt{\lambda_r}} T' D\sqrt{P_{i.}}\mathbf{f}_r$$

For the i th individual-point and the j th parameter-point, we have the following relation:

i th component of $\mathbf{f}_r$

$$f_r^i = \frac{1}{\sqrt{\lambda_r}} \sum_{j=1}^p \frac{P_{ij}}{P_{i.}} g_r^j \quad i = 1, 2, \dots, n$$

j th component of $\mathbf{g}_r$

$$g_r^j = \frac{1}{\sqrt{\lambda_r}} \sum_{i=1}^n \frac{P_{ij}}{P_{.j}} f_r^i \quad j = 1, 2, \dots, p$$

f_r^j is at the gravity centre (with an approximation of $1/\sqrt{\lambda_r}$) of the p g_r^j values ($j = 1, 2, \dots, p$).

g_r^j is at the gravity centre (with an approximation of $1/\sqrt{\lambda_r}$) of the n f_r^i values ($n = 1, 2, \dots, n$).

inferring the graphical simultaneous representation of the two sets.

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Deux méthodes d'analyse multidimensionnelles ont été appliquées à l'étude biométrique du crâne, dans tout l'Ordre des Primates, à l'exception des Hominoidea. Les Prosimiens, en raison de leur forte hétérogénéité, ont été analysés plus particulièrement.

L'Analyse Factorielle des Correspondances pour 16 variables a permis une excellente répartition de sous-groupes allant souvent jusqu'au niveau du genre.

L'analyse discriminante a fait ressortir l'importance de l'opposition crâne cérébral/appareil masticateur dans tout l'Ordre et à tous les niveaux taxinomiques et a révélé que la largeur de la base du crâne possède un très fort pouvoir discriminant dans la comparaison de la forme du crâne de tous les Primates.

Il semble donc que nous pourrions, dans nos recherches ultérieures, utiliser ces méthodes pour placer des specimens fossiles dans la variation morphologique de l'Ordre, avec une probabilité d'erreur assez faible et à l'aide d'un nombre de meusurations très limité.

S. K. Bearder
G. A. Doyle

Department of Psychology,
University of the Witwatersrand,
South Africa

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Field and Laboratory Studies of Social Organization in Bushbabies (*Galago senegalensis*)*

During the course of a one year field study of the Lesser Bushbaby (*Galago senegalensis moholi*), using a technique of direct observation with red light, it was discovered that family groups which slept together during the daytime split up at night, with each member spending most of the time alone. During the night individuals would come into contact with one another or with members of adjacent groups and the resulting social behaviour varied considerably. An interpretation has been made of more than 120 interactions observed in the field based on the behaviour of bushbabies introduced to one another under controlled semi-natural conditions.

1. Introduction

One of the most important characteristics of Primates is their social nature. They live in social groups which remain quite stable over long periods and within which the individual learns much of the behaviour which adapts it to life in a particular environment and social setting (Dolhinow & Bishop, 1970). The primitive nocturnal prosimians, in contrast to diurnal Primates, are predominantly solitary in their habits and their social behaviour is somewhat less complex. However they frequently sleep together in family groups during the day and they meet one another at night, when they display a variety of social acts. Laboratory studies of artificial groupings which are larger than would normally be found in nature indicate that this primitive type of social organization may have given rise to more complex social groups.

The behaviour of the Lesser Bushbaby (*Galago senegalensis moholi*) has been studied in its natural habitat as well as in the laboratory, where the animals may be manipulated under controlled conditions. An attempt has been made to determine those factors, both behavioural and sensory, which may be important in the social organization and spacing out of this nocturnal prosimian.

A detailed account of communication in *Galago senegalensis* is given by Anderson (1969) who discusses many types of social behaviour which are relevant to the present study.

2. Field Observations

Data were collected during a one year field study in the thornveld savanna of the Northern Transvaal in South Africa. Approximately 500 hr of direct observation were made on 160 bushbabies by means of red light from a 6 V head torch and a hand lantern. Nests and sleeping places were found during the day. A census of 119 sleeping places showed that 40 % were used by a single animal and the remainder by groups of up to six individuals. Haddow & Ellice (1964) found that in 42 sleeping groups which they examined, 10 had no fully adult male present, 29 had one fully adult male present and only 3 contained two fully adult males. Of the bushbabies which they found sleeping alone, 26 were males and 13 were females.

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Within the study area bushbabies were loosely organized into "family groups". A "family group" may be defined as consisting of those animals whose individual ranges coincided or overlapped to a large extent and who would share the same sleeping place, at least on occasions. Such a group did not act as a social unit at night and a distinction may be made between individual and composite ranges. The composite ranges of neighbouring "groups" overlapped only to a small extent, if at all, and they were thus spaced fairly evenly within the available habitat. Some members of the "group" showed possible territorial behaviour in the form of olfactory marking, vocal advertisement and overt aggression towards rival conspecifics, but the existence of a territory in the sense of an area defended against encroachment by conspecifics (Burt, 1943) was not established.

The home ranges of bushbaby "groups" were found to have an average size of 2.8 ha within which were areas of frequent use. The "groups" showed less long term stability than in most Primate species and the range boundaries changed during the year. It is possible that male/female pairs remained in association for longer periods.

Social interactions in the wild followed the same pattern as those seen in the laboratory which often made it possible to deduce the age, sex and status of the individuals concerned. The total of 120 interactions which were witnessed may be divided into nine types in order of relative frequency.

As would be expected, friendly social contacts between familiar bushbabies were the most common interactions seen. Agonistic encounters with strangers were less frequent, while types 8 and 9 occurred only in particular restricted situations.

Social contacts at night occurred during 30 % of the total observation time. They were typically brief, including those between a mother and her infants, but occasionally one animal would follow another for a period of a few hours. Friendly contact was generally initiated when one bushbaby approached the other which usually descended the tree. Naso-nasal and ano-genital sniffing often took place at the base of the tree or on the ground. Friendly interactions included contact urine-washing, grappling, chasing, play and periods of vigorous alternate grooming. In agonistic situations the subordinate animal always descended to the ground and generally made a variety of calls and fled if chased. Overt fighting was not common. Wild bushbabies were not seen to suffer from the typical loss of fur which occurs during serious fights in the laboratory.

Several laboratory born bushbabies were released into the wild in order to observe whether their behaviour was affected by captivity and to test the reactions of wild adults to their presence. It was found that their range of movement was extremely restricted, they were not wary of potential predators, they spent an unusual amount of time on the

Type of interaction	Situation in which it occurred
1. Friendly approach	} Predominantly intra-group encounters
2. Friendly chasing	
3. Mother/infant contact	
4. Mutual avoidance	} Predominantly inter-group encounters
5. Aggressive chasing	
6. Overt fighting after aggressive chasing	
7. Overt fighting after mutual approach	} Restricted situations
8. Aggressive chasing by female with infants	
9. Chasing of a female by a male prior to mating	

ground searching for food and they sometimes slept near to the ground, unlike any wild bushbaby. Wild males were persistent and friendly in their attentions to laboratory females, none of which was in oestrus, but were aggressive towards the males. Fighting occurred between wild males and laboratory males, which moved very little. The wild males returned repeatedly and both animals vocalized when close by.

3. Social Behaviour in the Laboratory

It has been noted by Jolly (1966) that bushbabies, *G. senegalensis* and *G. crassicaudatus*, are social animals but with a far less integrated group and less well differentiated individual rôles in the group than even caged lemurs. In fact, as has been pointed out, the term group is only loosely applicable in the case of *G. senegalensis*. It is evident that the laboratory situation in which family units are confined to relatively small cages, where solitary movement is impossible, is not a natural one. Yet despite the fact that agonistic behaviour is often much more common in captivity than in the wild (Gartlan, 1968), it was found that bushbabies could remain together for long periods with very little agonistic behaviour, providing they were grouped in family units. Given sufficient space it is possible to establish unnaturally large groupings in captivity (Doyle & Bekker, 1967), and Manley (1966) found no aggression between the males of two pairs which were housed together. Infants were invariably perfectly integrated into the group and remained so even when mature.

In our laboratory situation there was generally no readily apparent dominance hierarchy between members of a group, but occasionally fighting broke out as the offspring matured. When two strangers were brought together from different groups social dominance was shown through agonistic behaviour.

In order to determine the nature of dominant/subordinate relationships, a series of diadic introductions was performed between strangers of different age/sex classes in a variety of environments.

Methods

A detailed description of the maintenance and housing of the laboratory bushbabies is given by Doyle & Bekker, (1967).

Essentially the laboratory consists of a central observation room on either side of which are two cages measuring approximately 2 m $\times$ 2 m $\times$ 2.5 m each. These contain branches and nest boxes and form the home environments for groups of up to six bushbabies. Additional animals are housed in stock cages.

An altered day-night cycle enables observations to be made during the daytime under red light. White lights are turned on automatically after 12 hr. All observations are made through one-way mirrors separating the four cages from the observation room which remains in darkness. Microphones are installed over each cage to relay all sounds to the observation room where they may be recorded. Behavioural records are made on an Esterline-Angus 20-channel continuous events recorder.

The test animals were divided into four age/sex classes; adult males (300 days +), sub-adult males (200–300 days), adult females (200 days +) and juveniles (60–200 days). A diadic analysis was made for the interactional possibilities which can occur between

these classes as given by the formula

$$\frac{N(N-1)}{2} \quad (\text{Carpenter, 1965})$$

Forty-three individuals of different classes were used in a series of 130 pair introductions each lasting for 40 min. Each pair of strangers was observed in three separate environmental situations in order to assess the effect of the environment on their behaviour. These were: the home cage of one, the home cage of the other and a neutral cage. The exact age, weight and previous associations of each test animal were recorded together with a breakdown of the Esterline-Angus record and a list of the calls which were made. Twenty-four units of data were obtained for each bushbaby during every session. Observations were also made on individuals which were returned to their home group after a session, and of strangers which were introduced into a stable group.

Social acts

Auditory patterns. No attempt is made to describe the various calls which are given by bushbabies. Extensive use is made of signals utilizing the acoustical communicatory channel, with fairly discrete calls as would be expected in a nocturnal arboreal animal (Moynihan, 1967; Marler, 1965; Altmann, 1967). Units of discrete calls may be mixed in order to convey a variety of mood messages (Andersson, 1969). Andersson has recorded a repertoire of 23 to 25 calls for this species (Table 1) of which 15 were heard during agonistic encounters, all being uttered by the subordinate animal. At least 7 of these were also heard in alarm situations. Only one call was given by an aggressor but this occurred very rarely. A dominant bushbaby often gave the "male" call or made "soft hoots" during friendly chasing.

The "male" call has considerable social significance (Andersson, 1969). It was originally thought to be confined to adult males but has subsequently been heard from adult females in the laboratory when they are dominant within a cage. It is commonly heard at the beginning of the active period and may be given at odd intervals throughout the night. Generally an adult male will start the call and it will be answered by others in adjacent cages. Maturing males do not call as frequently or as loudly as do older (generally heavier) males (Andersson, 1969).

Field data show that this call is most common soon after sunset during the birth and mating seasons, particularly in areas having a high population density. At other times of the year it is seldom heard. It is given by females with young infants and by males while they are stationary or on the move. Two or more animals may answer one another for long periods and they generally remain apart. The call was also heard when given by males as if "calling" for a companion at dawn. It seems that the "male" call advertises the presence of an assertive adult and acts as a spacing mechanism with the result that intra-specific fighting is largely avoided. The calls are quite loud and have been shown by Andersson (1969) to exhibit both the low frequencies and sharp repetitive characteristics considered important for distance communication by Marler (1965). Several other Primates are known to use calls as an aid to spacing, with examples such as the *Hylobates* (Ellefson, 1968) and *Callicebus* (Mason, 1968). Among the prosimii it is a characteristic of *Galagoides*, (Cansdale, in Hill, 1953) *G. crassicaudatus* (Bearder & Doyle, 1972) and several species of lemur (Petter, 1962).

Table 1.

Social acts

<i>Auditory patterns</i>			
1. Grunts	7. Explosive-cough	13. Sneezes	19. Plaintive yap
2. Spits	8. Bark (Male call)	14. Gerwhit	20. Yap alarm
3. Chatter	9. Soft hoot	15. Cluck	21. Wuffs
4. Moans	10. Coo	16. Shivering-stutter	22. Wails
5. Screams	11. Soft grunt	17. Whistles	23. Caws
6. Rasp	12. Squeaks	18. Yap	24. Clicks/Crackle
<i>Visual patterns</i>			
A. Facial expressions		B. Body postures and movements	
1. Defensive threat		1. Swaying	
2. Defensive attack		2. Cringing	
3. Fighting		3. Tail positioning	
4. Offensive threat		4. Tail lashing	
		5. Presenting	
		6. Nose licking	
<i>Olfactory patterns</i>			
A. Deposition of odouriferous substances		B. Social sniffing	
1. Urine-washing		1. Naso-nasal sniffing	
2. Rhythmic micturition		2. Ano-genital sniffing	
3. Chest/head rubbing			
4. Chin and mouth rubbing			
<i>Contact patterns</i>			
A. Friendly contact		B. Agonistic Contact	
1. Naso-nasal, naso-anal contact		1. Holding, grasping	
2. Allogrooming		2. Biting	
3. Play wrestling		3. Kicking	
4. Mounting		4. Fur pulling	
5. Infant transport			
6. Nursing			
7. Huddling			

Visual patterns. Although *G. senegalensis* has extremely sensitive night vision and highly developed powers of accommodation (Luck, 1963), it has been shown by Andersson (1969) that the large repertoire of facial expressions and body postures, that constitute an extensive visual communication system in the higher Primates, does not occur in this species. She describes four facial expressions and six body postures which are listed in Table 1.

Olfactory patterns. Olfactory cues may be expected to play a more important rôle in communication in the prosimii than in the higher Primates as is evidenced by their moist rhinarium, relatively large olfactory lobes and the widespread occurrence of special scent glands (Montagna & Ellis, 1959, 1960; Montagna & Yun, 1962; Montagna, 1962). Andersson (1969) notes various marking and rubbing movements as well as social sniffing for *G. senegalensis* (Table 1).

There are several indications that the sense of smell plays the most important rôle in intra-specific recognition in common with many other primitive mammals (Marler, 1965; Charles-Dominique, 1971). Adult male bushbabies show considerable interest in adjacent cages if they contain other adult males. Fighting is often attempted through small cracks in the partition causing damage to the fingers. If one of these males enters the cage of the other they fight almost immediately, irrespective of which other animals are present. Bushbabies which avoid one another in an initial encounter will frequently

sniff at those places where the other has been sitting and contact is always accompanied by direct sniffing. The motivation of a subordinate to smell a dominant animal is high, even if it results in antagonism.

Adult males mark females by contact urine-washing. This occurs especially when a female is returned to her home cage after a short absence or when a strange female is introduced to a male. There is some evidence that males show greater antagonism towards females that have been marked by other males than to those which have not.

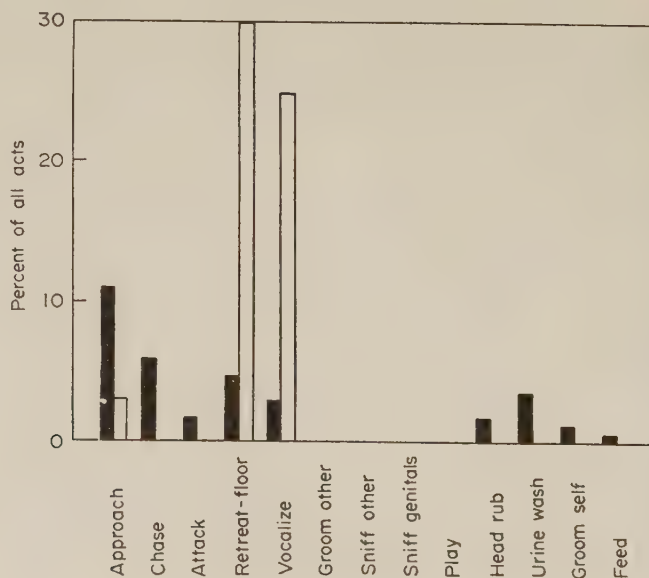
Contact patterns. Despite the relatively solitary behaviour of *G. senegalensis*, compared with many Primates, a number of contact patterns have been recorded during social encounters, and individuals may huddle together during the daytime sleep. Unlike the higher Primates where the hand is used to initiate physical contact (Marler, 1965), the naso-nasal or naso-anal contact of the "lower" mammals is still the most common form of greeting behaviour in the bushbaby (Andersson, 1969). Allogrooming occurs frequently in a wide variety of circumstances and it is not restricted to sexual situations. In accordance with observations in many other primates, allogrooming not only cleans the skin and fur but also acts as a social bonding ritual that helps to reduce tension and aggressive tendencies, while it facilitates other reactions involving contact (Andersson, 1969).

Diadic interactions

Adult male/adult male (Figure 1). When a male was placed in the home cage of another male he tried to avoid the resident which soon attacked causing the stranger to flee onto the floor while making vocalizations. The subsequent fighting did not lead to serious physical injury.

When strange males were introduced by removal of a partition between their adjacent home environments, both animals were highly aggressive and severe wounds were

Figure 1. Frequency distribution of acts during ten 40-min encounters between strange adult males. ■ Dominant; □ subordinate.



sustained through fighting. Such fights were the only agonistic encounters which occurred without vocalizations. When one of the combatants had been thoroughly beaten it would escape and begin to make a number of calls. It is evident that mutual recognition occurred almost immediately and the nature of the dominant/subordinate relationship depended largely on familiarity with the environment.

Adult male/sub-adult male (Figure 2). Adult males were not aggressive to sub-adults and in fact these interactions were often quite friendly. Mature adults were more friendly than were the younger ones. This "benevolence" was also noticed with their behaviour towards females.

Sub-adult male/sub-adult male (Figure 3). Sub-adults showed considerable mutual antagonism and would sometimes fight, but without causing serious damage. One of the two would usually vocalize. The highest levels of aggression occurred when the age difference between the pair was small, with the older animal being dominant irrespective of its relative size, or environmental factors. Maturity was evidently of considerable importance in affecting these interactions.

Adult male/adult female (Figure 4). Adult males dominated females in all situations, even when they were smaller. Their behaviour was always friendly although sometimes quite rough. The females at first rejected the attentions of the male by fleeing and emitting low intensity calls which increased in intensity if the male was rough. Later they sometimes allowed themselves to be groomed and marked with urine. The older males were quieter and more successful in their approaches towards the females than the younger ones.

Sub-adult male/adult female (Figures 5 and 6). The pattern of these introductions falls clearly into two types. When males were dominant they were invariably friendly, although somewhat rough. When the females were dominant they were always highly aggressive. The nature of the interaction was then similar to that between adult females. The age of the male was the most important factor which influenced the position of

Figure 2. Frequency distribution of acts during 14 40-min encounters between strange adult males and sub-adult males. (Adult males dominant.) □ Dominant; ■ subordinate.

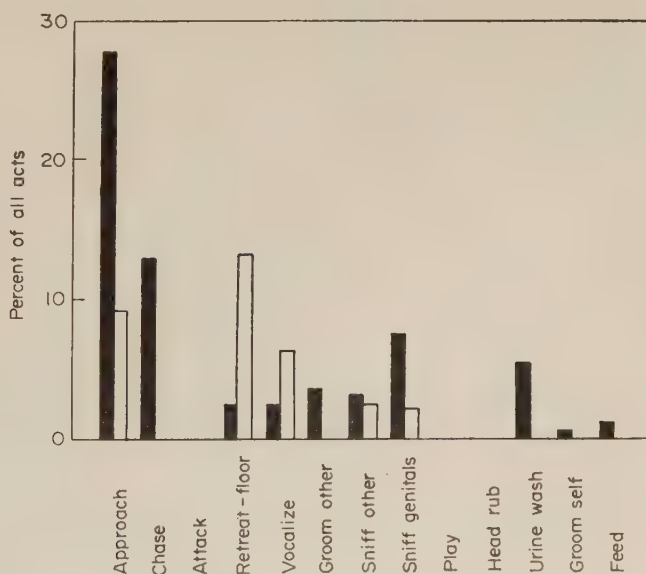


Figure 3. Frequency distribution of acts during nine 40-min encounters between strange sub-adult males. ■ Dominant; □ subordinate.

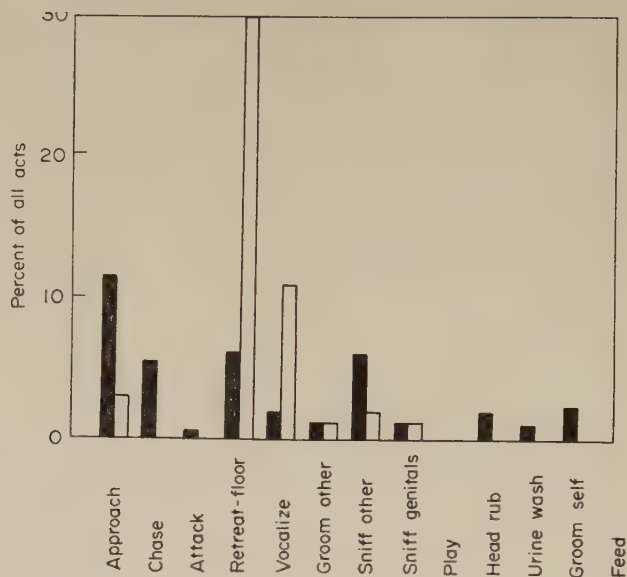


Figure 4. Frequency distribution of acts during 20 40-min encounters between strange adult males and adult females. (Adult males dominant.) ■ Dominant; □ subordinate.

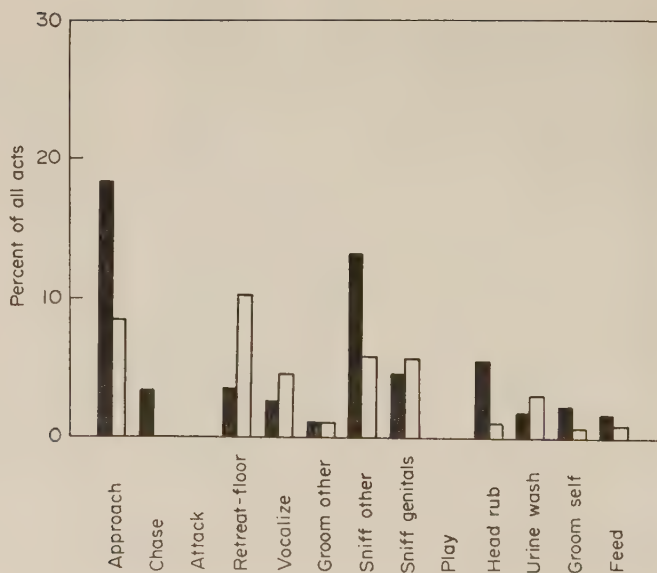


Figure 5. Frequency distribution of acts during 15 40-min encounters between strange sub-adult males and adult females. (Sub-adult males dominant.)
 ■ Dominant; □ subordinate.

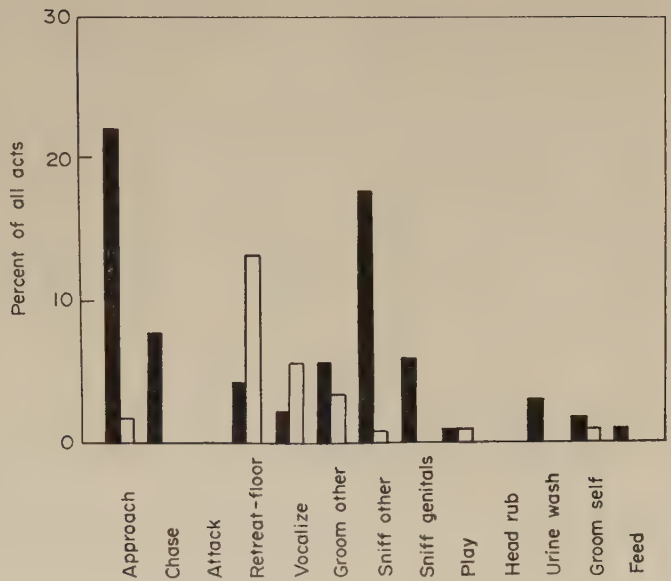
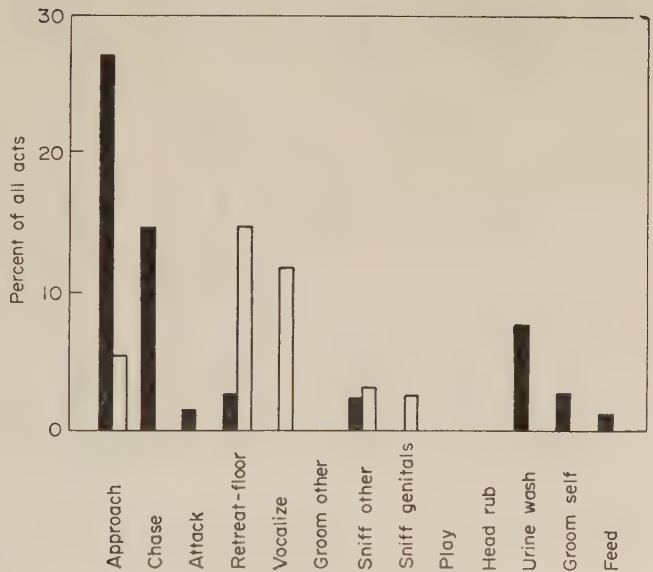


Figure 6. Frequency distribution of acts during 12 40-min encounters between strange sub-adult males. (Adult females dominant.)
 ■ Dominant; □ subordinate.



dominance. The sub-adult class represents a transition stage of increasing maturity from juvenile to adult. As the juvenile male begins to mature he is no longer tolerated by a strange adult female until he is old enough to dominate her, but he is still accepted by adult males. Full maturity is reached between 300 and 340 days when he begins to make the "male" call and is no longer accepted by other males.

Adult female/adult female (Figure 7). All introductions between adult females results in one of the two being highly aggressive and the other completely subordinate. The position of dominance became clear very quickly when one animal chased and attacked the other which retreated onto the floor while making a variety of high intensity calls.

Certain females were usually dominant in any environment while others were generally submissive. Relative size did not effect the position of dominance. Pregnant females and those with small infants were often unusually aggressive, even to the point of attacking the adult male in their home cage. In one case a death resulted from a fight between strange females.

Interactions involving juveniles (Figures 8 and 9). All age/sex classes were tolerant of juveniles and they frequently showed friendly interest accompanied by mutual smelling and grooming, with occasional bouts of play. Juveniles would approach adults many times out of curiosity but sometimes the mere presence of a stranger would cause a nervous juvenile to spend the entire observation session on the floor giving alarm calls. Certain juveniles seemed to pass through periods of nervousness during their development.

When two juveniles were placed together they avoided contact while showing obvious interest in one another. They did not smell or groom each other.

Introduction of an individual into a group. When a stranger was introduced into a stable family group or when an individual was returned to its own group after a short period of absence, there followed a period of olfactory "checking" of the newcomer and between members of the group. A dominant stranger sometimes caused considerable confusion

Figure 7. Frequency distribution of acts during 23 40-min encounters between strange adult females. ■ Dominant; □ subordinate.

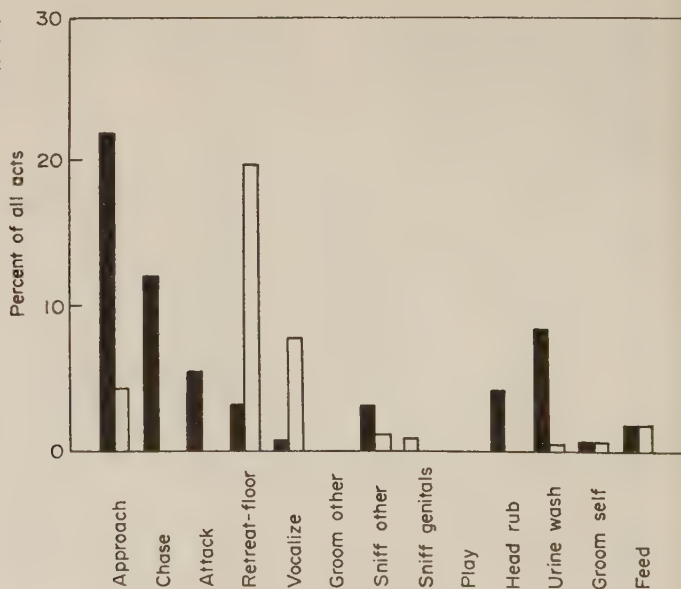


Figure 8. Frequency distribution of acts during 19 40-min encounters between strange adults or sub-adults and juveniles. (Adults or sub-adults dominant.) ■ Dominant; □ subordinate.

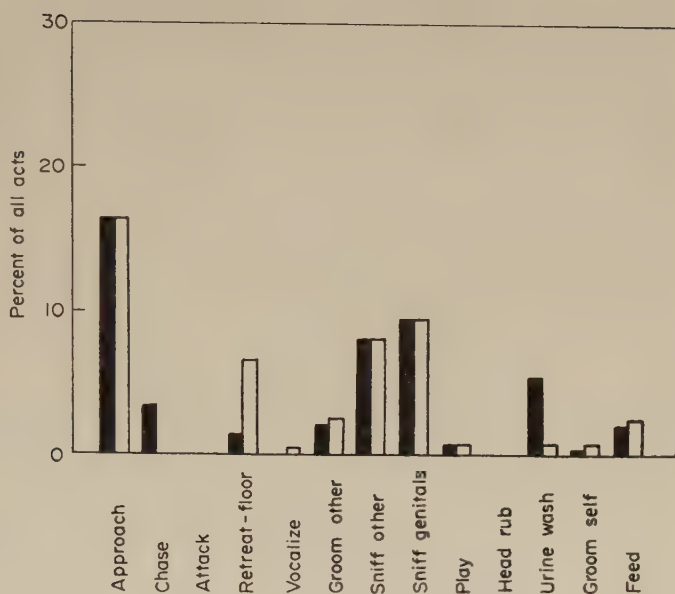
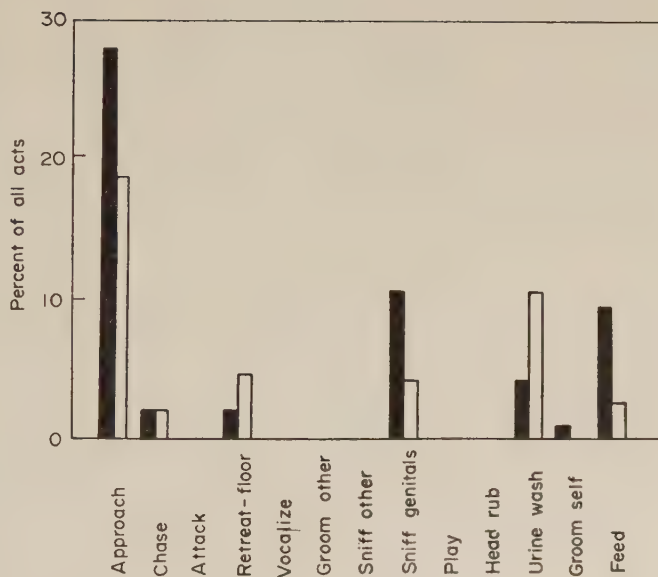


Figure 9. Frequency distribution of acts during eight 40-min encounters between strange juveniles. □ Dominant; ■ subordinate.



and group members became wary or frightened, to the extent that fighting would break out between previous companions. The behaviour of a stranger to individual group members followed the patterns described above.

When an absentee was reintroduced into its group it settled down more quickly than a stranger which often took several hours before being accepted, if at all. The period of separation necessary to erase individual recognition was difficult to establish, but this is evidently an important consideration which affects the social interactions between individuals.

4. Discussion

An underlying pattern emerges from the behaviour observed during introductions, yet the results represent an oversimplification of the social behaviour of bushbabies, as there were some exceptions to the general rule for each diadic interaction.

Introductory sessions may be divided into those which were hostile and those which were amicable. As with tree shrews during hostile encounters (Kaufmann, 1965), subordinate bushbabies relied on threatening signals and avoided contact while dominants remained relatively silent and initiated physical attacks. The dominant animal typically approached, chased and attacked while the subordinate spent more time on the floor and gave a variety of vocalizations. In addition dominants urine-washed, head-rubbed, groomed and fed more frequently than subordinates. During amicable encounters the dominants more often approached and chased the subordinates which again vocalized and spent more time on the floor. Other behaviours showed no characteristic pattern.

A bushbaby in an unfamiliar environment usually began to explore by smelling all accessible parts of the cage. Adult males also rubbed their chests against projections or sharp edges, frequently biting the wood after each rubbing movement. Females occasionally rubbed the sides of their mouths against objects, and both males and females urine-washed. Olfactory exploration and marking did not occur if the individual was frightened by the presence of a stranger.

A combination of visual, olfactory and auditory clues are used by a bushbaby in order to recognize the status of a stranger. The nature of each introduction was controlled by the behaviour of the dominant animal, depending on whether it was friendly, aggressive or ignored the stranger. The position of dominance was in turn determined primarily by the age and sex of the animals concerned and to lesser extent by their previous associations, knowledge of the environment and individual differences in character. These factors combined to modify the status of an animal in such a way that a bushbaby which was placed in a strange environment after having suffered a beating from a conspecific, would be subordinate even to members of its own family group over which it usually dominated. The initial position of dominance between strangers could be reversed, given sufficient time, as the newcomer became more settled and familiar with the environment.

Several factors are evidently in operation on controlling the types of association which occur between individuals in the wild and their spacing within the available habitat. It has been demonstrated in the laboratory that strangers of the same age/sex class are generally incompatible and adult females do not tolerate young males as they begin to mature. Yet associations between these classes may still occur providing the individuals remain familiar with one another. It seems probable that as the young mature their

ranges become increasingly separate from those of the parents with a corresponding decrease in mutual familiarity. Should the range of a maturing individual come to overlap that of a stranger then they may interact in a way that has been described. Pair bonds may develop between males and females through the persistent attentions of the male, while some individuals may be forced out of the ranges of others through antagonism. It can be seen that the older and generally heavier males will be more successful in developing and maintaining pair bonds, both by their quieter approach and by their dominance over other males.

The separation of rivals is probably maintained by the use of the "male" call. In addition bushbabies mark one another and their environment with urine and possibly by chest rubbing and these olfactory clues may carry information regarding the presence of particular individuals in an area, even though they do not act as markers of a defended territory.

A social way of life may confer several advantages on a species as described by Dolhinow & Bishop (1970). Youngsters can learn the subtleties of communication, food habits, which paths are used for travelling from one place to another, which trees provide suitable sleeping places and which animals are dangerous. Social behaviour also enables individuals to become familiar with other members of the community in which they live.

The social system of *G. senegalensis* allows it to take advantage of many of these features but not to the same extent as in those Primates living in organized social groups which function as a unit. In common with many primitive mammals bushbabies are by contrast predominantly solitary during their active period and communicate by means of olfaction and auditory signals more than by visual displays and expressions. Similar social structures are found in a variety of nocturnal primates including *Galagoides demidovii*, *Galago alleni*, *Eutoticus elegantulus*, *Perodicticus potto*, *Lepilemur mustelinus* and *Microcebus murinus* (Charles-Dominique, 1971; Martin, 1968). The Aye-Aye (*Daubentonia madagascariensis*) appears to be more completely solitary (Petter, 1962) while the Thick-tailed Bushbaby (*G. crassicaudatus*) and the nocturnal species of monkey (*Aotus trivirgatus*) are both slightly gregarious (Bearder & Doyle, 1972; Moynihan, 1967). The social behaviour of *G. senegalensis* illustrates a situation which could easily lead to the formation of cohesive groups but such groups seem to have reached their full development only in the diurnal Primates.

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Carlo Maxia

*Institute of Anthropological Sciences,
University of Cagliari, Italy*

Giovanni Floris

*Department of Anthropology,
University of Sassari, Italy*

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Dermatoglyphics in Endogamic Populations of Sardinia

Several dermatoglyphic characteristics (palmar and plantar) of different populations in Sardinian communities are reported. Graphs illustrating the dermatoglyphic behaviour of the single communities examined are presented.

It can be seen that each community behaves differently from the others, even when they are geographically close together. Sexual differences appear quite accentuated in some communities while in others they are negligible. From the present study, as well as from other studies on the hereditary characteristics of Sardinians, it emerges that Sardinia is in reality subdivided into many different populations, or endogamic stocks, each presenting a particular behaviour of its own, sometimes quite different from that presented by the other populations.

The study of dermatoglyphs, hereditary characteristics, as yet little understood, which take on their final form in about the fourth month of intra-uterine life, is a great help toward a better knowledge of the different human populations. Thus dermatoglyphs can be added to the numerous other anthropological characteristics used in the diagnosis of race and, above all those Mendelian hereditary characteristics such as blood groups and P.T.C. sensitivity, which are not influenced by the environment.

Sardinia is an excellent area for dermatoglyphic examination because its inhabitants, most of them at least, through historical events and geographical factors, have undergone less mixing with different peoples and thus present a characteristic genoma all their own.

Furthermore, within the limits of the Sardinian population, as Maxia has demonstrated in different researches, single populations or endogamic groups are to be distinguished and these groups, at least since prehistoric times, have remained isolated from one another. Thus reproduction has occurred only within the group itself. Hence, the study of dermatoglyphs can be used to show, as is already done for blood groups, the genoma characteristics of the various populations which are different and, in some cases, quite different (even though geographically close together).

The results presented here were obtained from the examination of several palmar and plantar dermatoglyphic characteristics. In 56 communities palmar dermatoglyphs were recorded and 30 communities were examined for plantar dermatoglyphs. These communities belong to the 15 historical-geographical areas into which Sardinia has for some time been divided and altogether 6110 individuals (3142 males and 2968 females) were examined for palmar dermatoglyphs and 2025 (972 males and 1053 females) for plantar dermatoglyphs.

In the following pages, data are given in the 12 Figures regarding the single communities examined for: (a) main line index (in the single sexes and overall) (Figures 1 and 2); (b) ratio of the frequency of true patterns (and vestiges) present in the hypothenar and thenar/I interdigital areas (Figure 3); (c) interdigital pattern index (Figure 4); (d) rudimental stages (X) and absence (0) of the "C" line (Figure 5); (e) a-b ridge count (Figure 6); Streng triangle for the modal types of lines "D" and "A" (Figures 7 and 8); (f) middle final field of line "D" (Figure 9); (g) main line plantar index (Figure 10); (h) absence of the triradius "p" (Figure 11); (i) frequency of the true patterns presenting higher values in the hallucal area (Figure 12).

Figure 1. Main line index (M and F).

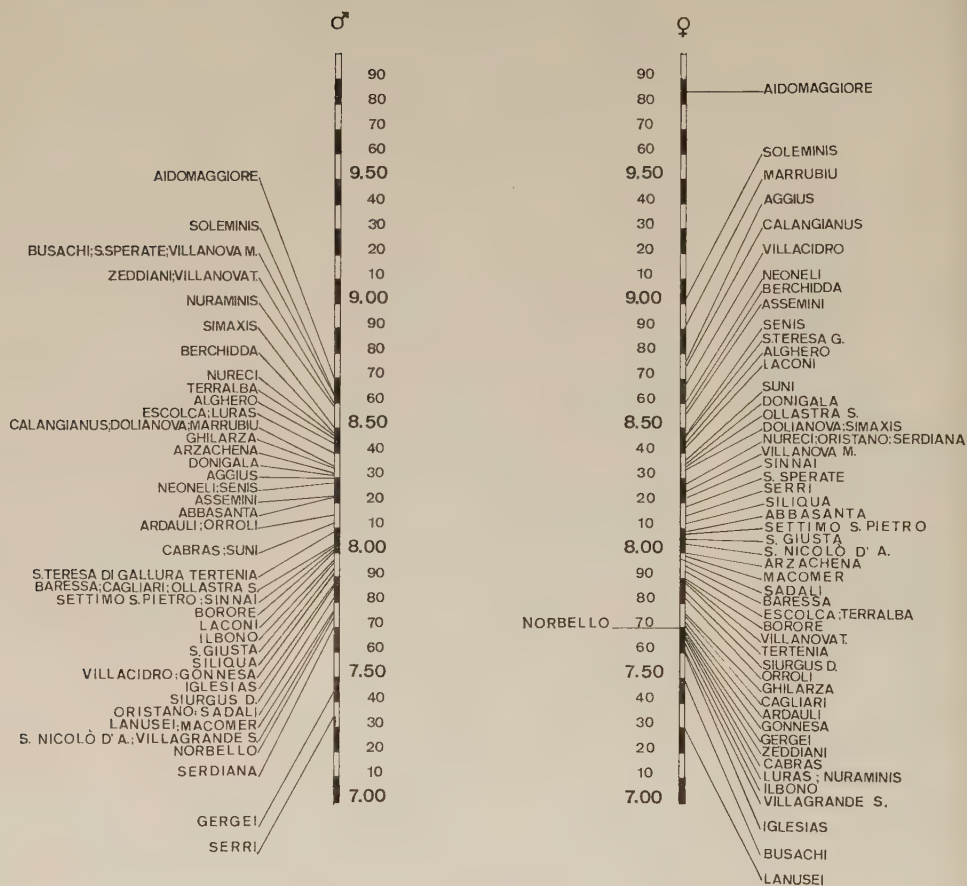


Figure 2. Main line index (M and F).

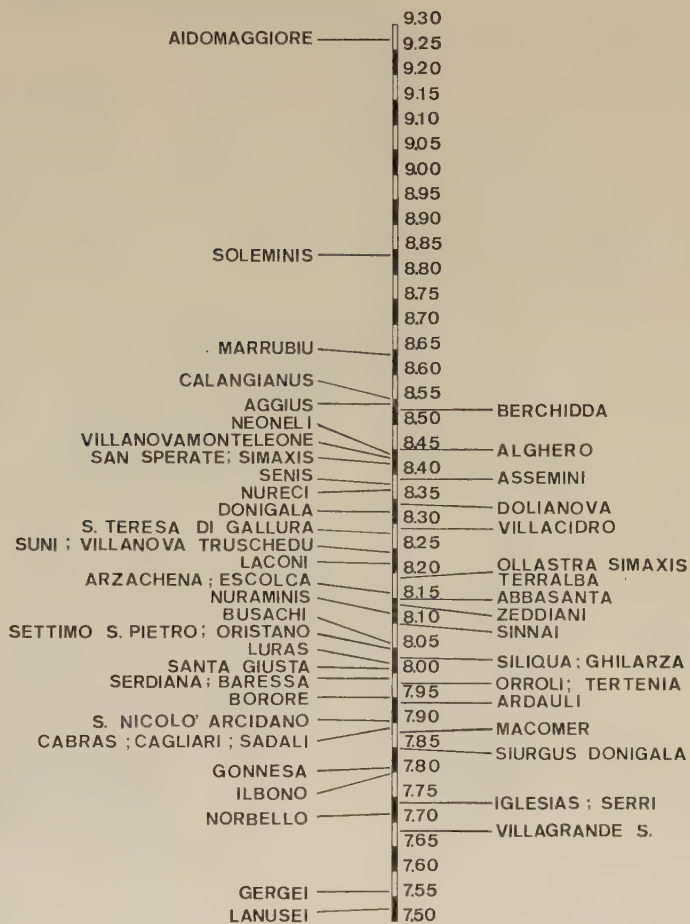


Figure 3. Ratio of true patterns (and vestiges).

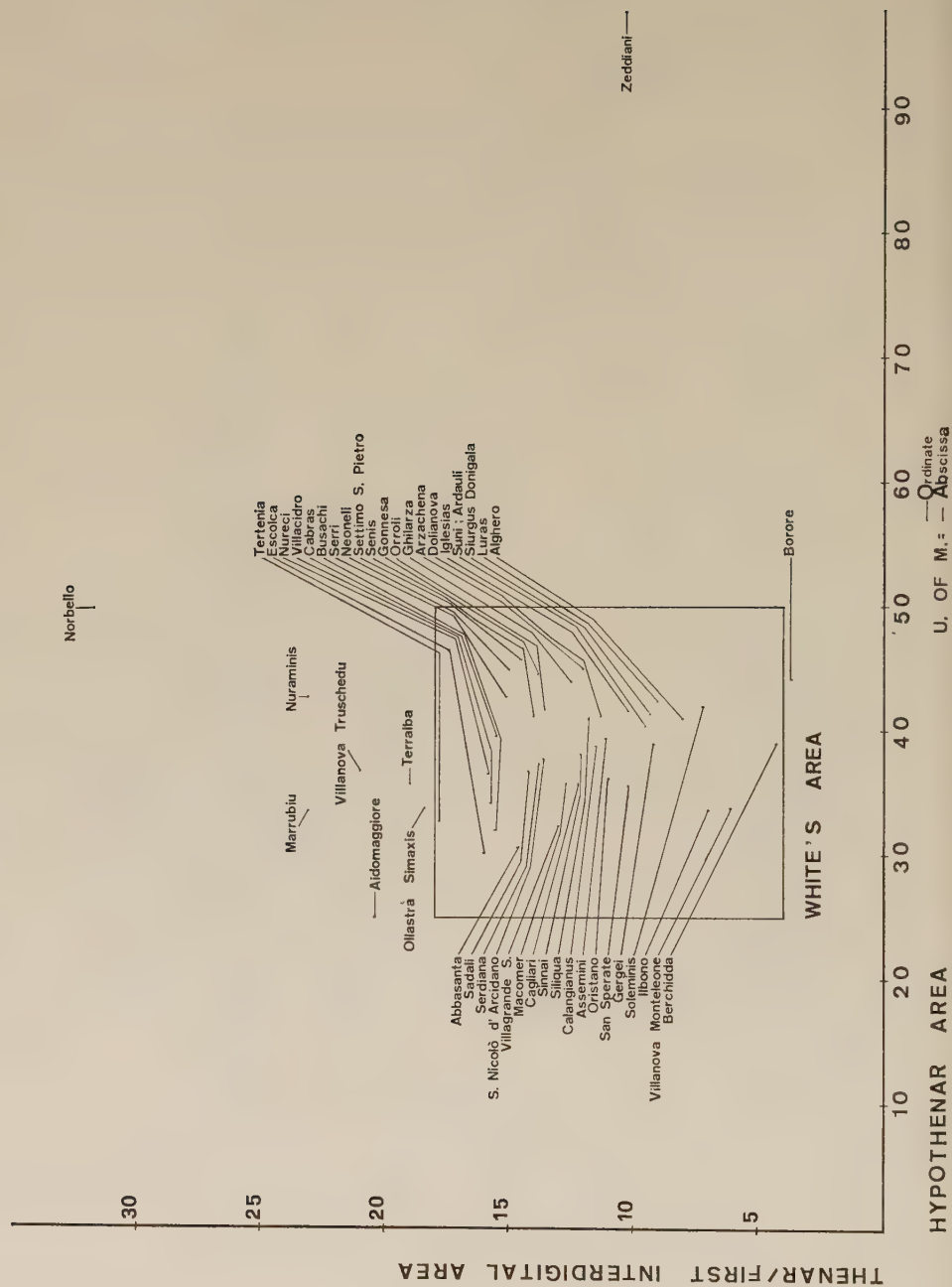


Figure 4. Interdigital pattern index.

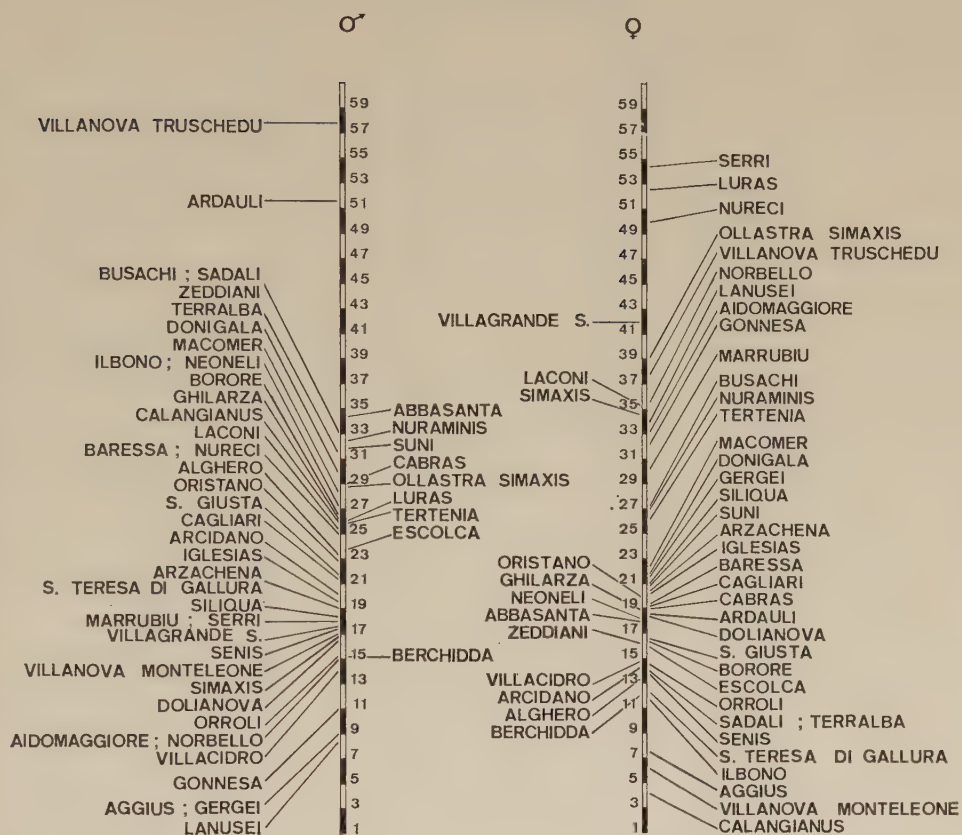


Figure 5. States (X) and 0 of line "C".

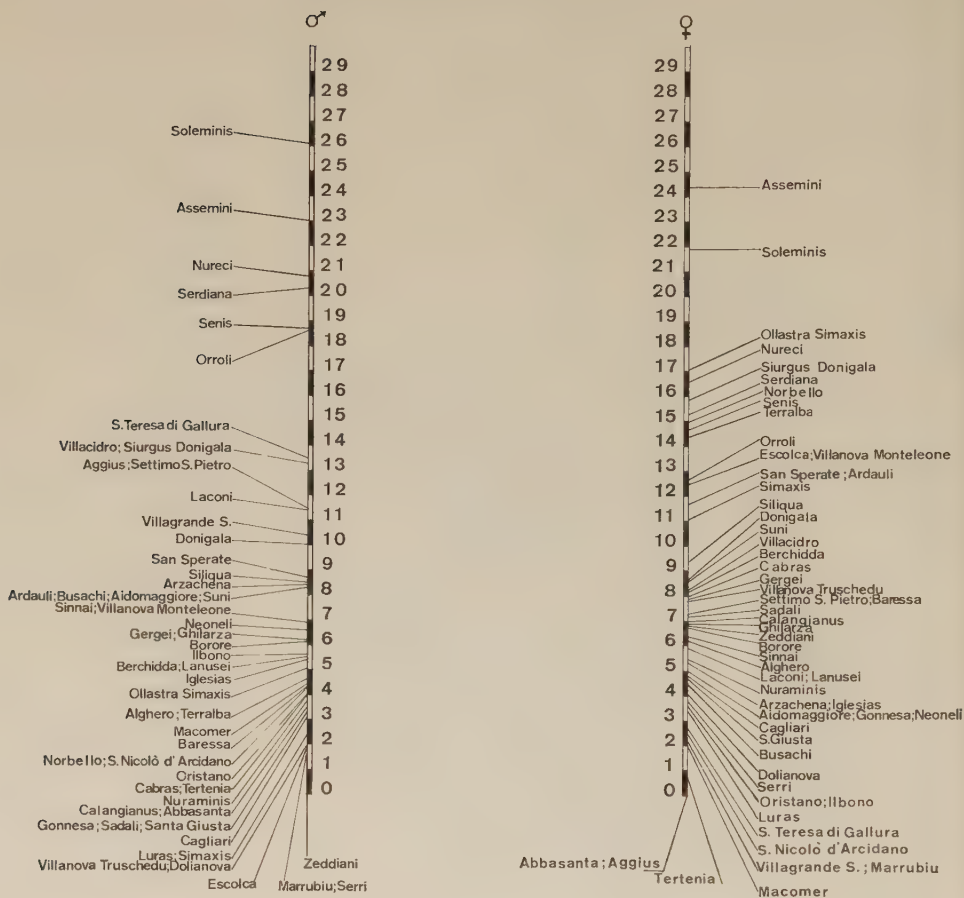


Figure 6. a-b ridge count.

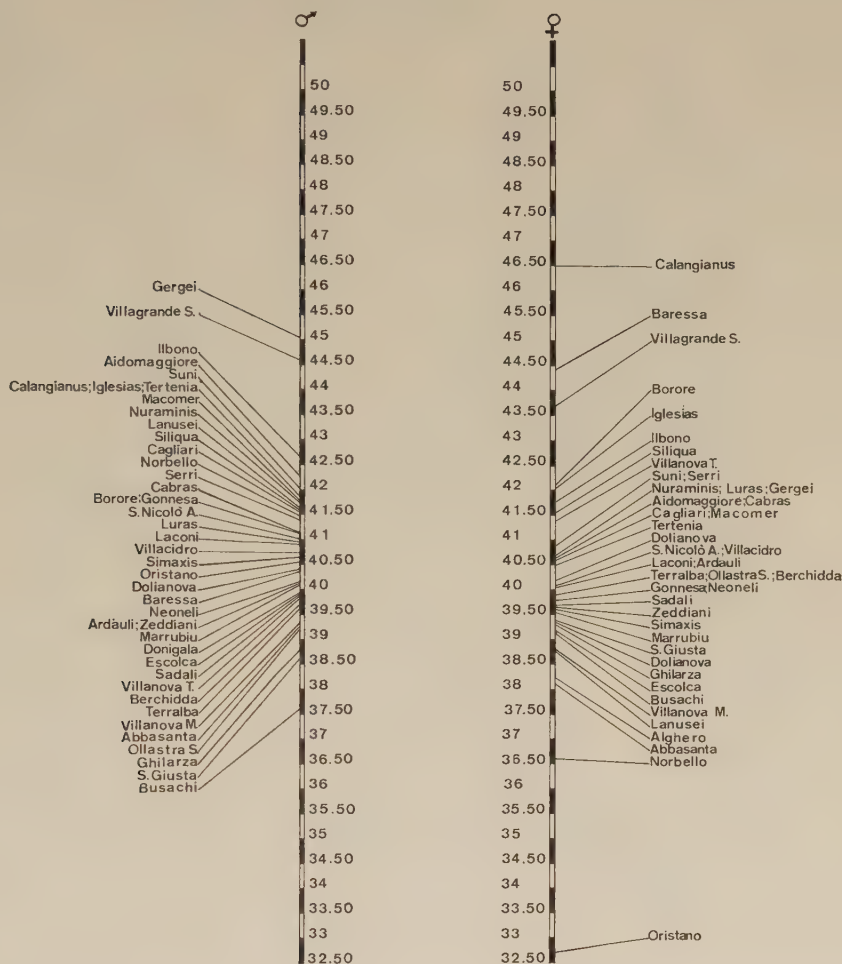


Figure 7. Modal types of line "D".

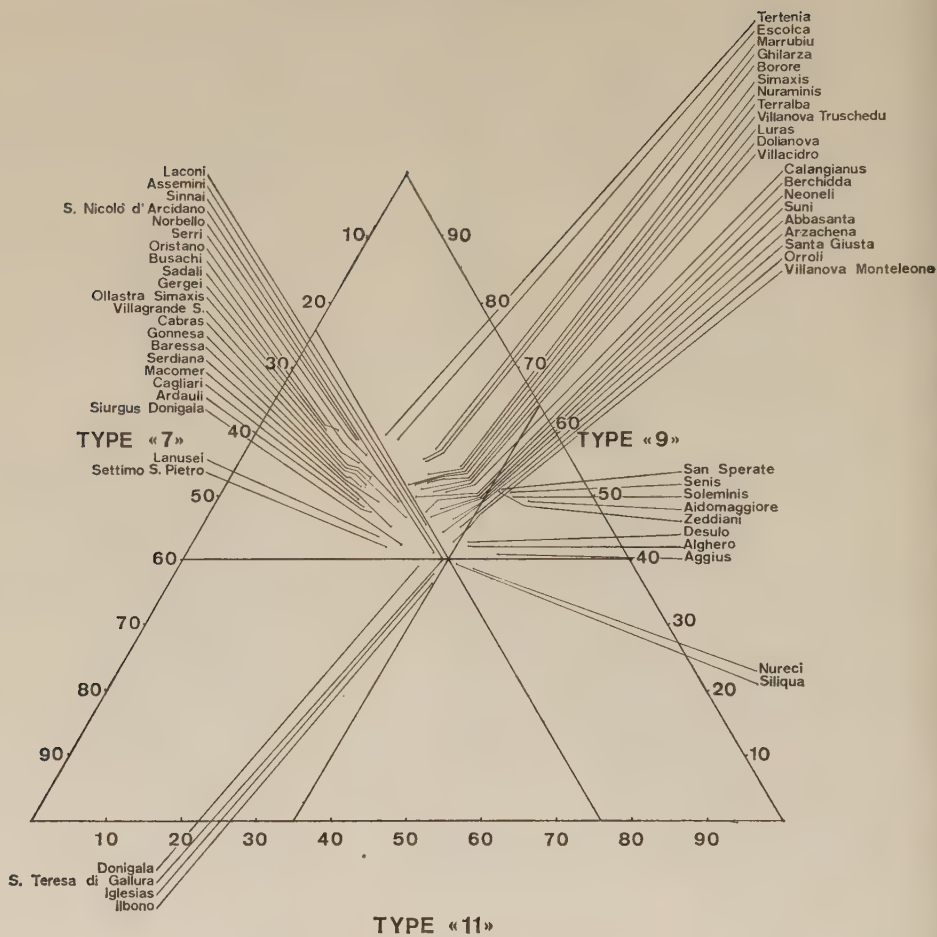


Figure 8. Modal types of line "A".

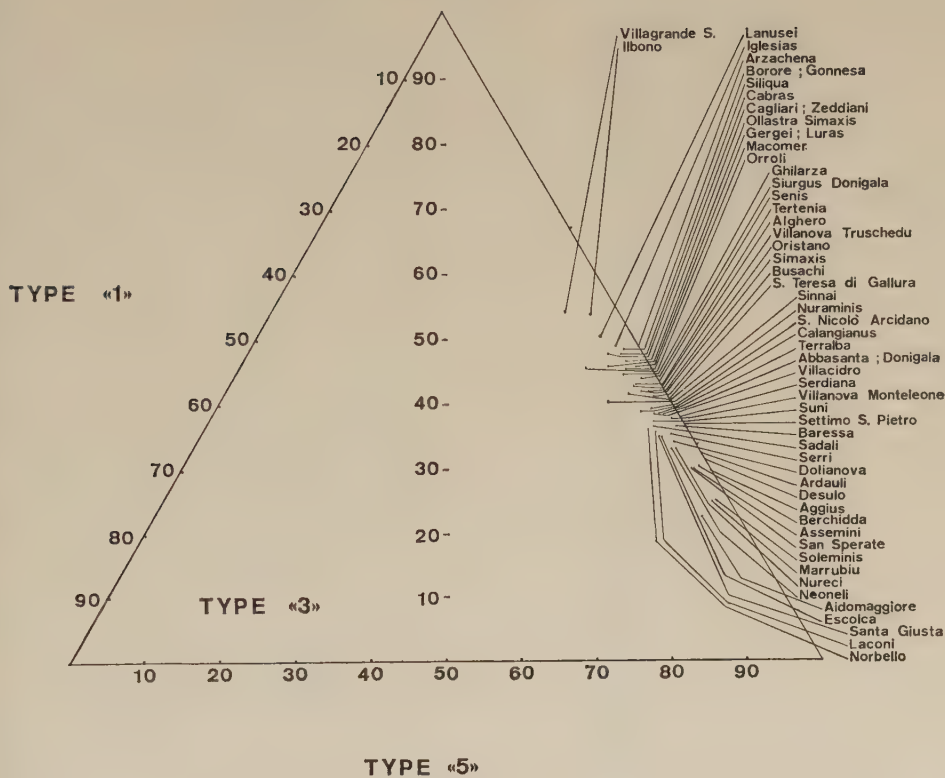


Figure 9. Middle final field of line "D" (MD).

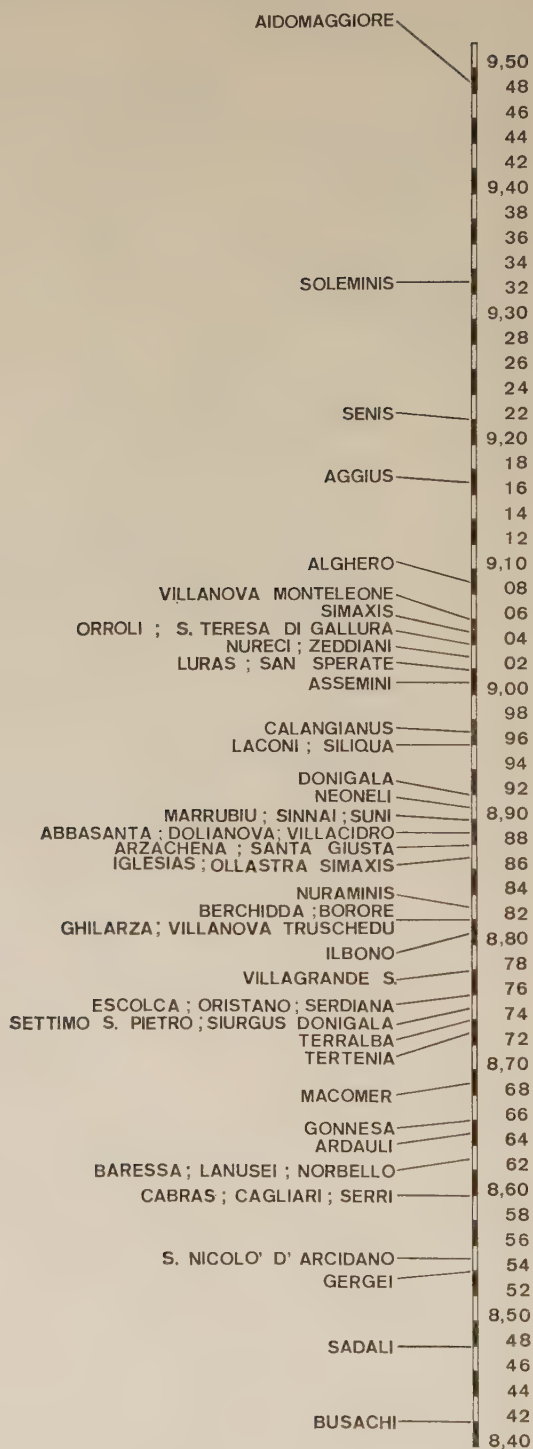


Figure 10. Main line plantar index.

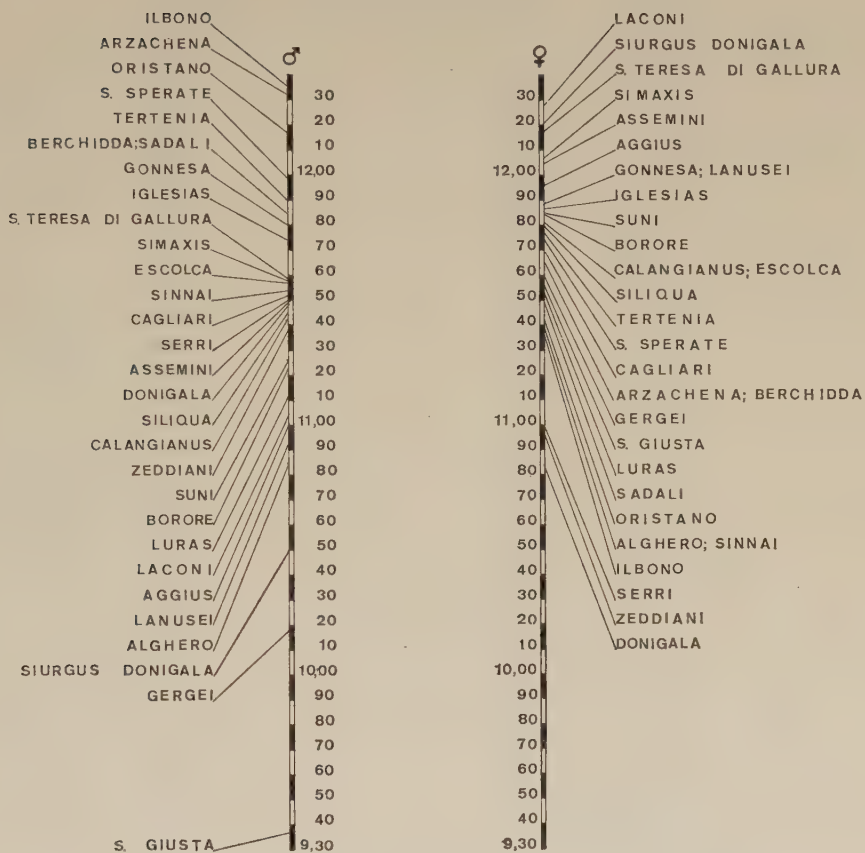


Figure 11. Absence of triradius "p".

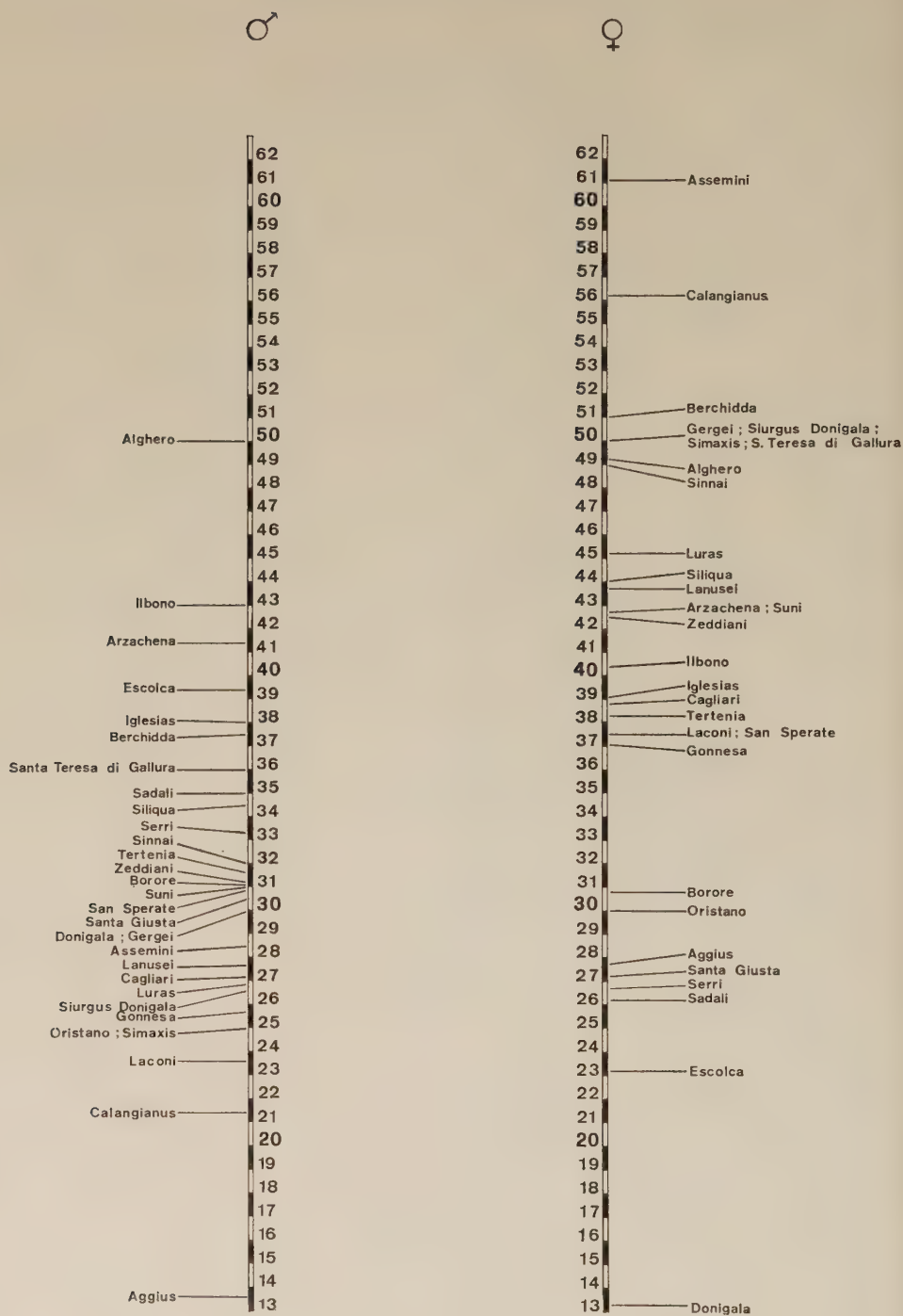
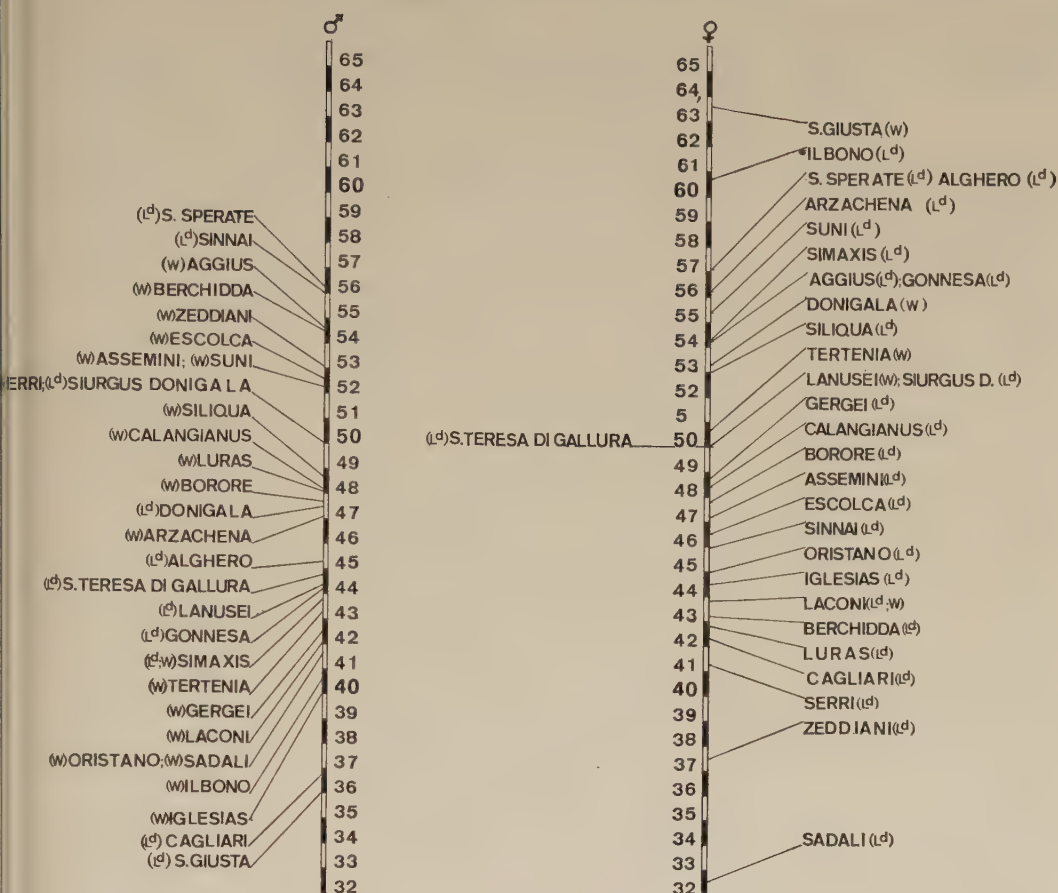


Figure 12. Frequencies of main types of configuration in the allucal area.



As appears evident from these figures, the different communities examined behave heterogeneously. For certain characteristics, some communities group together, with very slight differences, while for other characteristics groups of other communities are formed, and the groups thus formed usually have no geographical significance. Sometimes, a community behaves in such a way as to be defined as aberrant with respect to the others, although it is regarded as normal for other characteristics. Considerable sexual differences are found in some communities while in others they are not (see, for example in Figure 12, the different behaviour in the two sexes in the communities of Santa Giusta and Ilbono, while it is equal in Siurgus Donigala).

In particular, in Figure 3 we see the behaviour of those communities, 9 out of 56 (16.07%), which are outside the area of the Whites, and especially that of the community of Zeddiani. In Figure 7, the centering of the Sardinian populations in the intermediate higher and higher left sector of the triangle and the absence of populations in the intermediate lower sector (occupied by Mongol, Polynesian and Malagasey groups) are also shown. It is to be remembered that the Europoid groups are assembled in the lower right-hand sector where only 2 of the 57 Sardinian populations examined (3.51%) are living.

Summing up, each community has its own particular behaviour diverging from the others, which is proof of the different hereditary patrimony which distinguishes the communities themselves. Dermatoglyphic examination is quite adequate to show this act (as is also true for the analysis of blood groups and other hereditary characteristics).

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Book News

Included in this section are those books and journals which have been received for review, or of which we have otherwise been informed. The mention of a book in this section does not preclude subsequent review in the Journal.

The Structure of Human Populations

Edited by G. A. Harrison & A. J. Boyce. 1972. London: Oxford University Press at the Clarendon Press. A vol. in-8°, xvi + 448 pp., figs, tabs, bibl., index. Bound £7.00, paper £3.00.

This book provides a very valuable basis for examining the inter-relationships between biological and social phenomena in human groups, and contains contributions from demographers, population geneticists, sociologists and ecologists. It will be useful to both students and teachers in the Human Sciences generally.

Contents

Foreword: F. Fenner.

The framework of population studies—G. A. Harrison and A. J. Boyce; *Geographical influences upon the size, distribution, and growth of human populations*—John I. Clarke; *Patterns of human fertility and mortality*—Gordon F. De Jong; *Perspectives in historical demography*—Michael Drake; *Social regulation of fertility*—Burton Benedict; *Factors associated with the sex ratio in human populations*—Michael S. Teitelbaum; *Mathematical models in demography*—R. W. Hiorns; *Migration, exchange, and the genetic structure of populations*—G. A. Harrison and A. J. Boyce; *Genetic implications of population breeding structure*—William J. Schull; *Behaviour and mating patterns in human populations*—James N. Spuhler; *Social mobility*—A. H. Halsey; *Natural selection in mankind*—Theodosius Dobzhansky; *Genetic aspects of the demography of American Indians and Eskimos*—Francisco M. Salzano; *Tribal social organization and genetic microdifferentiation*—Napoleon A. Chagnon; *Demography of small scale societies*—Colin M. Turnbull; *Demography, ecology, social structure, and settlement patterns*—Peter Kunstadter; *Demographic variables as measures of biological adaptation: a case study of high-altitude human populations*—Paul T. Baker and James S. Dutt; *Ecology and population structure in the arctic*—William S. Laughlin; *Tropical ecology and population structure*—Joseph S. Weiner; *Ecology in relation to urban population structure*—Stephen Boyden.

Paralipomena Mongolica

(Veröffentlichungen des Museums für Völkerkunde zu Leipzig, 19). By J. Schubert. 1971. Berlin: Akademie Verlag. A vol. in-8°, 326 pp., ill., bibl., index. Paper DM29,50.

Resulting from fieldwork done in 1957–1966, this comprehensive volume is an ethnographical report on the Peoples' Republic of Mongolia. The book is written in German.

Journal of Human Evolution (1974) **3**, 65–97.

Contents

Einleitung; Die Natur; Zur Geologie: Allgemeines, Stratigraphie und Tektonik, Magmatismus (Vulkanismus und Seismik), Metalle (chemische Elemente), Minerale, Gesteine, Mineralquellen (Mineralwässer); Zur Paläontologie: Paläobotanik, Paläozoologie; Zur Paläogeographie; Zur Geographie: Allgemeines, Kartographisches, Hydrographisches, Orographisches, Klimatologisches; Zur Botanik; Zur Zoologie: Insecta, Pisces, Reptilia, Aves, Mammalia; Der Mensch; Zur Anthropologie; Zur Ur- und Frühgeschichte; Der Mensch als Individuum; Zur Geschichte: Die Familie, Familienverband, Stämme und Völker, Sprachen und Dialekte, Der Staat, Siedlungen, Lebensweise und Kultur, Wirtschaft, Religion; Benutzte Literatur; Übersicht über die mongolischen Ausdrücke; Liste der chinesischen Zeichen; Nachlese; Chronologische Tabellen 1154–1368; Bildanhang.

The Biology of Alcoholism

Edited by B. Kissin & H. Begleiter. 1971–1972. New York & London: Plenum Press. 2 vols in-8°, LX + 1182 pp., figs, tabs, bibl., index. Cloth £32.70

These first two of a three volume work contain the most comprehensive examination to date of current knowledge on the biological mechanisms involved in the development of alcoholism. The authors are all leading authorities on various aspects of alcoholism, and their several contributions are carefully organized so as to emphasize and explore the biological interaction between ethanol and animal at different levels of activity. A valuable reference work.

Contents

Vol. 1: Biochemistry. Absorption Diffusion, Distribution, and Elimination of Ethanol: Effects on Biological Membranes—H. Kalant. The Metabolism of Alcohol in Normals and Alcoholics: Enzymes—J. P. von Wartburg. Effect of Ethanol on Intracellular Respiration and Cerebral Function—H. Wallgren. Effect of Ethanol on Neurohumoral Amine Metabolism—A. Feldstein. The Role of Acetaldehyde in the Actions of Ethanol—E. B. Truitt, Jr. & M. J. Walsh. The Effect of Alcohol on Carbohydrate Metabolism: Carbohydrate Metabolism in Alcoholics—R. A. Arky. Protein, Nucleotide, and Porphyrin Metabolism—J. M. Orten & V. M. Sardesai. Effects of Ethanol on Lipid, Uric Acid, Intermediary, and Drug Metabolism, Including the Pathogenesis of the Alcoholic Fatty Liver—C. S. Lieber, E. Rubin & L. M. De Carli. Biochemistry of Gastrointestinal and Liver Diseases in Alcoholism—C. M. Leevy, A. K. Tanribilir & F. Smith. Alcohol and Vitamin Metabolism—J. J. Vitale & J. Coffey. The Effect of Alcohol on Fluid and Electrolyte Metabolism—J. D. Beard & D. H. Knott. Mineral Metabolism in Alcoholism—E. B. Flink. Alcohol-Endocrine Interrelationships—P. Stokes. Acute and Chronic Toxicity of Alcohol—S. W. French. Biochemical Mechanisms of Alcohol Addiction—J. H. Mendelson. Methods for the Determination of Ethanol and Acetaldehyde—I. Sunshine & N. Hodnett. The Chemistry of Alcoholic Beverages—C. D. Leake & M. Silverman.

Vol. 2: Physiology and Behaviour. Effects of Alcohol on the Neuron—R. G. Grenell. Peripheral Nerve and Muscle Disorders Associated with Alcoholism—R. F. Mayer & R. Garcia-Mullin. The Effects of Alcohol on Evoked Potentials of Various Parts of the Central Nervous System of the Cat—H. E. Himwich & D. A. Callison. Brain Centres of Reinforcement and Effects of Alcohol—J. St-Laurent. Factors Underlying Differences in Alcohol Preference of Inbred Strains of Mice—D. A. Rogers. The Determinants of Alcohol Preference in Animals—R. D. Myers & W. L. Veale. Voluntary Alcohol Consumption in Apes—F. L. Fitz-Gerald. State-Dependent Learning Produced by Alcohol and Its Relevance to Alcoholism—D. A. Overton. Behavioural Studies of Alcoholism—N. K. Mello. The Effects of Alcohol on the Central Nervous System in Humans—H. Begleiter & A. Platz. Changes in Cardiovascular Activity as a Function of Alcohol Intake—D. H. Knott & J. D. Beard. The Effect of Alcohol on the Autonomic Nervous System of Humans: Psychophysiological Approach—P. Naitoh. Alcohol and Sleep—H. L. Williams & A. Salamy. Alcoholism and Learning—M. Vogel-Sprott. Some Behavioural Effects of Alcohol on Man—J. A. Carpenter & N. P. Armenti.

Analytical Archaeology

By D. L. Clarke. 1968. London: Methuen & Co. First paperback edition, 1971. A vol. in-8°, xx + 684 pp., 170 figs, bibl., index. Paper £3.50.

This book marked in 1968 the emergence of a new configuration for the "undisciplined empirical discipline" of archaeology. Its paperback edition is very welcome.

Contents

Preface. *Introduction and Polemic*: The history of archaeology, The nature of archaeology, The nature of archaeological data, The aims of archaeology, Terminology, definition and meaning, Models, Summary. *Culture Systems—the Model*: Systems theory, an outline, A tentative general model, Discussion, Summary. *Cultural Morphology and Cultural Ecology—the Setting*: The nature of cultural systems, Culture as an information system, Culture as a system with subsystems, Environment as a system with subsystems, Summary. *Material Culture Systems—Attribute and Artefact*: Introduction, Attribute and artefact systems, Phase pattern regularities, Time pattern regularities, System pattern regularities, Summary. *Artefact and Type*: Introduction, Artefact-type systems, phase pattern regularities, Time pattern regularities, System pattern regularities, Summary. *Assemblage and Culture*: Introduction, Cultural assemblage systems, Phase pattern regularities, Time pattern regularities, System pattern regularities, Summary. *Culture and Culture Group*: Introduction, Culture group systems, Phase pattern regularities, Time pattern regularities, System pattern regularities, Summary. *Culture Group and Technocomplex*: Introduction, Technocomplex systems, Phase pattern regularities, Time pattern regularities, System pattern regularities, Summary. *Group Ethnology*: Introduction, Internal evidence, Recent ethnographic evidence, Historical ethnographic evidence, Summary. *Summary—Entities and Processes*: Introduction, Entities, Processes, Procedure. *Methods of Analysis*: Models and approach, Time trends, Space trends, Strategies, Summary. *Numerical Taxonomy and Statistical Aids*: Introduction, Numerical taxonomy, Statistical aids, Summary. *Computer Methods and Examples*: Introduction, Examples, Summary. *Summary and Conclusions*: Theoretical background, Disciplined procedure, Archaeological grammar, Sociocultural models, Speculations. Definitions.

The Megalithic Art of the Maltese Islands

By M. Ridley. 1971. Christchurch: The Dolphin Press. A vol. in-4°, 32 pp., 76 pls, bibl. Cloth.

This is a descriptive inventory of Maltese megalithic art, in which all the relief carvings, the engravings and the paintings are brought together for the first time. An atlas for workers involved with the study of prehistoric Maltese society.

Contents

Foreword—F. S. Mallia. Introduction. Megalithic art. Plates 1–76. Catalogue to the plates.

Der Ursprung des Menschen. Unser gegenwärtiger Wissensstand

By G. Heberer. 1972. Stuttgart: Gustav Fischer Verlag. 3rd ed. A vol. in-16°, 72 pp., 35 figs, bibl. Paper DM6.80.

This is a revised edition of Professor Heberer's well known précis of human evolution.

Die gesellschaftlichen Verhältnisse der Ewe-Bevölkerung in Südost-Ghana

(Veröffentlichungen des Museums für Völkerkunde zu Leipzig, 22). By A. Asamoah. 1971. Berlin: Akademie Verlag. A vol. in-8°, 228 pp., ill., bibl. Paper.

This ethnographical report covers a useful body of data on the economy and social organization of the Ewe group of Southeastern Ghana. The text is written in German.

Contents

Vorwort; Einführung: Das Gebiet der Ewe. Geographie und historischer Überblick unter besonderer Berücksichtigung der Landschaften Sokode Klefe und Taviefe—Geographie des Ewe-Gebietes im allgemeinen, Die unmittelbare landschaftliche Umgebung und die Anlage von Sokode, Klefe und Taviefe, Zur Geschichte und zur Entwicklung von Wirtschaft und Sozialstruktur in der Vorkolonialzeit, Der geschilderte Entwicklungsprozeß am Beispiel der untersuchten Dörfer, Die Beziehungen zwischen Ho und den umliegenden untersuchten Dörfern. Die gegenwärtige ökonomische Situation in den untersuchten Dörfern—Die Technik und Arbeitsorganisation in den verschiedenen Wirtschaftszweigen, Die Eigentumsverhältnisse, Die untersuchten Familien von Sokode, Klefe und Taviefe, Auswertung und Ergänzung des vorgelegten Materials. Verwandtschaftsstruktur, politische und soziale Verhältnisse in den drei Dörfern—Die Verwandtschaftsgruppen, Die Kernfamilie, Die Verwandtschaftsstruktur in den drei Dörfern, Die politische Organisation, Die Position des Häuptlings in den drei untersuchten Dörfern, Gesellschaftliche Institutionen, soziale Schichten und Lebensweise.

Anhang I. Anhang II.

Nucleic Acid Hybridization in the Study of Cell Differentiation

Edited by H. Ursprung. 1972. Berlin, Heidelberg, New York: Springer-Verlag. A vol. in-8°, xii + 76 pp., figs, tabs, bibl. Cloth \$11.50.

This volume brings together six articles by investigators actively working on various aspects of developmental biology who use nucleic acid hybridization as a tool in their research. Both beginners and advanced students will find the book helpful for understanding the principles of the method, the various techniques that are used and the biological implications of the results already obtained.

Contents

The Problem of Genetic Identity of Different Cell Types—Heinz Tobler; *Tissue Specificity of Genetic Transcription*—R. B. Church and I. R. Brown; *Kinetic Analysis of the Base Sequence Heterogeneity of RNA Molecules by RNA/DNA Hybridization*—Ian Purdom, Robert Williamson, and Max Birnstiel; *Nucleic Acid Hybridization to Isolated Chromatin*—Ki-Han Kim; *Hybridization of Nucleic Acids to Chromosomes*—Dale M. Steffensen and D. E. Wimber; *Nucleic Acid Hybridization and the Nature of Chromosomal Protein Bound RNA*—Ru Chih C. Huang and M. Mitchell Smith.

Brain and Human Behavior

Edited by A. G. Karczmar & J. C. Eccles. 1972. Berlin, Heidelberg, New York: Springer-Verlag. A vol. in-8°, xii + 476 pp., figs, tabs, bibl., index. Cloth \$30.50.

This volume is based on the Symposium on *The Brain and Human Behavior*, held in October of 1969 as a part of the centennial observance of the Loyola University of

Chicago. One of the most challenging problems dealt with in this volume concerns the manner in which memory storage is brought about and the manner of its retrieval. This outstanding book is an attempt to bridge the biological, sociological and philosophical aspects of Man, brain and behavior.

Contents

Introduction. What we know now, will know in the future, and possibly cannot ever know in neurosciences—A. G. Karczmar. *Molecular and Synaptic Organization*: Molecular Organization of Synapses for Chemical Transmission in the Central Nervous System—E. de Robertis; Possible Synaptic Mechanisms Subservicing Learning—J. C. Eccles; Synaptic Modulations—A. G. Karczmar, S. Nish & L. C. Blaber. *Biochemical Mechanisms and Pharmacological Approaches*: Some Brain Protein Changes Reflecting Neuronal Plasticity at Learning—H. Hyden; Norepinephrine in Central Nervous System and Its Correlations with Behavior—S. S. Kety; Some Monoaminergic Mechanisms Controlling Sleep and Waking—M. Jouvet. *Neurophysiological Correlates*: Data Structure and Algorithms in the Primate Somatosensory Cortex: G. Werner, B. L. Whitsel & L. M. Petrucelli; Cortical Visual Areas and Their Interaction—M. Mishkin; Neurophysiological and Psychophysical Correlates in Vision Research—R. Jung; Integrative Properties of Parastriate Neurons—F. Morrell; Neural Correlates of Learning and Memory—E. R. John; Electrophysiological Correlates of Positive Reinforcement: Post-Reinforcement Synchronization, Modulation of Sensory Input, and Steady Potentials—T. J. Marczyński. *Psychological Aspects*: Nature, Nurture and the Psychological Approach to Learning—D. Bovet; Phylogeny of Memory Development in Vertebrates—I. S. Beritashvili. Time, Space, Motivation, Memory, and Decision—W. T. Liberson; The Ontogeny of Behavior and the Concept of Instinct—S. A. Barnett; Operational Structures of the Intelligence and Organic Controls—J. Piaget. *Epistemological Aspects*: In Defense of Teleology—R. Granit; The Mentality of Man's Brain—S. Toulmin; What Difference Does Mind Make?—E. McMullin; Conditions for a Mechanistic Theory of Behaviour—Ch. Taylor.

The Assessment of Population Affinities in Man

Edited by J. S. Weiner & J. Huizinga. 1972. Oxford: Clarendon Press. A vol. in-8°, xii + 228 pp., figs, tabs, bibl., index. Bound £6-00.

Comparison of human populations constitutes an important part of human biology and physical anthropology. The statistical methods for assessing biological distances in human populations have steadily become more refined and effective. This volume aims to bring to the attention of students, or those entering research in these fields, the wide array of techniques currently in use.

Contents

Preface—J. S. Weiner and J. Huizinga. Measures of taxonomic distance and their analysis—J. C. Gower; Comparison of different measures of genetic distance between human populations—L. D. Sanghvi and V. Balakrishnan; Affinity as revealed by differences in gene frequencies—A. W. F. Edwards and L. L. Cavalli-Sforza; On the reconstruction of evolutionary trees of human populations resulting from random genetic drift—M. B. Maljutov, V. P. Passekov and Y. G. Rychkov; Genetic, linguistic, and geographical distances in native North America—J. N. Spuhler; The analysis of multivariate biological distances between human populations: principles and applications to sub-Saharan Africa—J. Hiernaux; The use of Penrose's C^2_H for an intra-population and inter-population analysis of the Bedik of Senegal—J. Gomila; Genetical affinities between populations in Western Europe and Scandinavia—T. S. Constandse-Westermann; Biological distances between indigenous populations of Taiwan—C. K. Chai.

Pathology of Simian Primates

Edited by R. N. T-W-Fiennes. 1972. Basel: S. Karger. 2 vols in-8°, c + 1700 pp., 377 figs, 181 tabs, bibl., index. Cloth £69.30.

This comprehensive work, covering all aspects of simian pathology, comprises contributions from 67 experts from the USA, USSR, France, Switzerland and Britain. The aggregate of these numerous and varied papers in a series of interesting and well-documented theses, is not intended to replace other works on special aspects of simian medicine and husbandry, but rather to supplement them as a comprehensive and authoritative source of information.

Contents

Vol. 1: General Pathology

Natural History of Primates: *The Rational Use of Primates in Biomedical Experiments*—B. A. Lapin; *Phylogeny and Classification of Primates*—C. P. Groves; *Natural Diets of Wild Primates*—C. Jones; *Biological Normals*—B. A. Lapin & G. M. Cherkovich. Development, Growth, Nutrition and Metabolism: *Developmental Abnormalities*—A. H. Schultz; *Spontaneous and Induced Neoplasms in Nonhuman Primates*—R. W. O'Gara & R. H. Adamson; *The Pathology of Nutritional Deficiencies in Nonhuman Primates*—R. H. Wolf; *Red Cell Antigens of Primates*—J. Moor-Jankowski & A. S. Wiener; *Coagulation Fibrinolysis and Platelet Function*—C. Hawkey; *Stress*—C. W. Hill & C. E. Thomsen; *The Immunology of Nonhuman Primates*—R. T. Damian & N. D. Greene; *Autoimmune Diseases*—O. Felsenfeld; *Diseases of the Endocrine System*—H. G. Spies & M. T. Clegg; *Poisons and Toxins*—R. N. T-W-Fiennes. The Bodily Systems: *The Skin and Appendages, and Special Senses*—R. N. T-W-Fiennes. *Diseases of the Skeleton*—M. J. M. Barker & R. T. Herbert. *Skeletal Muscle Pathology in Non-Human Primates*—M. N. Golarz de Bourne & G. H. Bourne. *Diseases of the Nervous System*—K. R. Brizzee; *Diseases of the Oral Cavity*—B. Cohen & W. H. Bowen; *The Respiratory and Alimentary Systems*—R. N. T-W-Fiennes, B. A. Lapin, E. K. Dzshikidze & L. A. Yakovleva; *Liver Function and Disease in Primates*—S. M. Kruckenberg, C. E. Cornelius & J. E. Cook; *The Cardiovascular System*—W. P. McNulty & M. R. Malinow; *Blood Formation Disturbances in Monkeys*—B. A. Lapin & L. A. Yakovleva; *The Urinary System*—J. A. Roberts; *The Female Reproductive System*—D. C. Kraemer & N. C. Vera Cruz; *The Male Reproductive System*—J. A. Roberts.

Vol. 2: Infectious and Parasitic Diseases

Protozoa: *Protozoa of the Intestinal Tract*—R. B. Burrows; *Protozoa of Tissues and Blood (Other than the Haemosporea)*—J. R. Barker; *Plasmodium and Hepatocystis*—A. Voller; Helminths: *Nematodes of the Bowel and Tissues*—T. C. Orihel & H. R. Seibold; *Trematodes of the Intestinal Tract and Biliary Passages*—R. E. Kuntz; *Echinococcosis, Coenurosis, Cysticercosis, Sparganosis, etc.*—B. J. Myers; *Acanthocephala of Captive Primates*—G. D. Schmidt. Arthropods: *Ectoparasites and Vectors*—R. N. T-W-Fiennes. *Endoparasites—Lung Mites*—J. R. M. Innes & W. B. Hull; *Pentastomida*—J. T. Self & G. E. Gosgrove. Fungal and Bacterial Diseases: *Superficial Mycoses*—Y. Al-Doory; *Intermediate Mycoses*—Y. Al-Doory; *Systematic Mycoses*—Y. Al-Doory; *Spirocheta, Spirillum, Leptospira*—M. Pinkerton; *Treponema*—A. Fribourg-Blanc; *Enteropathogenic Organisms*—R. N. T-W-Fiennes, M. Pinkerton & E. K. Dzshikidze; *Respiratory Pathogens and other Organisms*—R. N. T-W-Fiennes & E. K. Dzshikidze; *Miscellaneous Organisms*—M. Pinkerton; *Tuberculosis*—R. N. T-W-Fiennes; *Anthrax, Fusiformis, Anaerobic Organisms*—B. D. Thorpe. Viruses and Small Organisms of Indeterminate Position: *Identification and Study of Viruses*—S. S. Kalter; *Serologic Surveys*—S. S. Kalter; *The Simian Picornaviruses*—R. L. Heberling; *The Simian Reoviruses*—R. L. Heberling; *The Arboviruses*—A. D. Felsenfeld; *Myxovirus and Pseudomyxovirus Groups*—G. D. Hsiung & N. S. Swack; *The Simian Adenoviruses*—R. L. Heberling; *The Herpesvirus Group*—M. D. Daniel, L. V. Meléndez, R. D. Hunt & B. F. Trum; *Pox Diseases in Primates*—W. P. McNulty; *Rabies*—R. N. T-W-Fiennes; *Infectious Hepatitis*—H. F. Smetana; *Infectious Hepatitis in Marmosets*—A. W. Holmes, L. Wolfe & F. Deinhardt; *Other Virus Diseases*—D. I. H. Simpson; *Chlamydiae and Rickettsiae*—L. F. Barker; *Oncogenic Viruses*—B. A. Lapin & L. A. Yakovleva.

Akten des Anthropologischen Kongresses, Mikulov (Tschechoslowakei) 1961

(Anthropos, N.S. 7, č. 15). Edited by J. Jelínek *et al.* 1963. Oosterhout: Anthropological Publications; New York: Humanities Press (for the Moravské Museum v

Brně). A vol. in-4°, 336 pp., ills, bibl. Cloth Dutch guilders 28.00.

Complete proceedings of a Czech symposium attended by many European scholars, mostly from the Eastern countries. Contents and underlying trends will prove of particular interest to physical anthropologists.

Contents

Préface—Jan Jelinek; *Vorrede*—Milan Dokládál; *Die Untersuchung der Körpergewebe am lebenden Organismus*—Bugyi Balázs; *Zur Beurteilung des Berufes und des Ernährungszustandes auf Grund von Knochenmaterial*—Bugyi Balázs; *Dimensions et Proportions somatiques des Athlètes des derniers jeux Olympiques (1960)*—Venerando Correnti; *Ein Beitrag zur Identifikation der Leichenbrände*—Milan Dokládál; *Contribution a l'Étude de la Croissance du Crâne du Chimpanzé*—Denise Ferembach; *Ergebnisse der anthropologischen auf der II. gesamtstaatlichen Spartakiade im Jahre 1960*—Vojtěch Fetter; *Characteristics and Evaluation of Child Obesity (in Russian)*—Vojtěch Fetter and Marie Horácková; *Anthropological Structure of a Medieval Novo Brdo Necropolis—Živojin Gavrilović; Anthropology of the Present and Ancient Population of Soviet Central Asia (in Russian)*—V. V. Ginzburg; *Puti migratsii žitel'ej mikronesii (in Russian)*—Alexandr Lech Godlewski; *Morfologické změny na kostrách obyvatelstva Čech za poslední tisíciletí*—Karel Hajniš; *Analyse des Méthodes de Calcul de la Capacité Crânienne d'après les Dimensions Linéaires*—Hodnocení výpočtových metod lebeční kapacity—Karel Hajniš; *Untersuchung der körperlichen Entwicklung der Schuljugend*—Věra Hladká; *Somatische Untersuchung der Schuljugend sowie der heranreifenden Jugend in der Gegend von Poděbrady (Mittleböhmen)*—Somatický průzkum školní a dospívající mládeže na Poděbradsku—Marie Hrubcová; *Anthropologie der Bronzezeit in Mähren*—Jan Jelinek; *Zuwachsrate und Ausbreitungsgeschwindigkeit bei den (Eu) Homininae, Ihre systematischen und Kulturgeschichtlichen Aspekte*—Gottfried Kurth; *Einige Fragen der Anthropolatonomie*—Pál Lipták; *Mathematischer Versuch zur Konstitutionstheorie*—Paul Lorenz; *Untersuchungen über Geschmackempfindungen, betreffend Phenylthiokarbamid, ausgeführt an Jugendlichen aus Debrecen (Ungarn)*—Mihály Malán und István Kacsur; *Über den Wert der Anthropometrie und der Konstitutionellen Typologie für die medizinische Forschung und Praxis*—Stanislav Mentl; *Incidence des Bronchites Récidivées sur le Développement somatique de l'Enfant*—Marie Nováková; *Anthropometrische Grundmerkmale und höchste sportliche Leistungsfähigkeit*—Vladimír Novotný; *Somatometrische Studie bezüglich der Tschechoslowakischen Basketball-Spielerinnen und Spieler*—Vladimír Novotný; *Repercussions anthropologiques du Système des Castes*—Georges Oliver; *Veränderungen der Körperstruktur bei longitudinaler Untersuchung von Kindern*—Jana Pařízková; *Körperhöhe und Handdruckkraft der Schüler in der Tiefebene und im Bergland*—Tibor Rajkaj; *Reflections about the Primatological Examinations of the Interior Organs*—Michal Reicher; *Zur Paläopathologie der hochmittelalterlichen slawischen Bevölkerung von Gustävel (Kreis Sternberg)*—H. Andersch and L. Schott; *New Results of anthropological Investigation of Youth Attending School*—Nové výsledky anthropologického zkoumání školní mládeže—Jaroslav Suchý; *Wertung der somatischen Typen von Frauen unter Benützung der Methode von B. Škerlj, J. Brožek, E. Hunt*—Svatava Titlbachová; *Les Saks (Scythes) des Environs de la Mer d'Aral (Nouveaux matériaux cranologiques)* (in Russian)—T. A. Trofimova; *Neue Ergebnisse zur Frage nach den verwandtschaftlichen Beziehungen der mitteldeutschen, böhmischen und mährischen Anjetitzer*—Herbert Ulrich; *Zur Fragen der Rassentypenbestimmung in den Leichenbrandgräbern (Kritik)*—Kotázka určování plemenného typu v žárových pohřbech (Kritika)—Emanuel Vlček; *Metrik und Morphologie in der anthropologischen Methodik*—Margarete Weninger; *Typology and Body-build forming in Polish Children and Adolescents from Towns and Villages*—Napoleon Wolański; *Anthropology and Ethnography in Research and Study of Human Society*—Josef Wolf; *Südmähren in der Geschichte der Anthropologie*—Jihomoravský kraj v dějích anthropologie—Vladimír Zapletal; *Morphologische Untersuchung der Warschauer Mädchen der Altersklassen zwischen 15 und 19 Jahren*—Maria Zdanska Brinckenowa.

Tools of Old and New Stone Age

By J. Bordaz. 1970. Garden City: The Natural History Press. A vol. in-16°, xiv + 146 pp., 54 figs, bibl., index. Paper \$2.95.

An introductory book about the stone implements of the Old World prehistory. Illustrations are abundant, but sometimes of inferior quality.

Contents

Preface. Introduction. Stone Tool Materials. The Core Tools: Choppers and Bifaces. Prepared Flake Nuclei: Levallois and Mousterian Flake Tools. The Blade Tools. Microliths and Ground Stone Tools. Key to Bibliography.

Human Populations, Genetic Variation, and Evolution

Edited by L. Newell Morris. 1971. San Francisco: Chandler Publishing Co. A vol. in-8°, xii + 500 pp., figs, tabs, bibl., index. Bound \$10.00.

This book of readings for university students is purportedly oriented toward a human population genetics seen from the viewpoint of physical anthropology. Each group of readings is preceded by an introductory overview; a brief glossary is added at the end of the volume.

Contents

Preface. *Introduction to population genetics*, Readings: The Hardy-Weinberg Law—Curt Stern; Mendelian Proportions in a Mixed Population—Godfrey H. Hardy; Four Achievements of the Genetical Method in Physical Anthropology—William C. Boyd.

The Population as a Unit of Study, Readings: Demographic Data on Two Xavante Villages: Genetic Structure of the Tribe—Francisco M. Salzano, James V. Neel and David Maybury-Lewis; Population Trends and Residential Segregation since 1960—Reynolds Farley and Karl E. Taeuber; Theories of Mate Selection—Bruce K. Eckland.

Mutation, Readings: Problems in the Assessment of Genetic Damage from Exposure of Individuals and Population to Radiation—Howard B. Newcombe; Mutations in Man—Friedrich Vogel; Human Population Cytogenetics—W. M. Court-Brown and P. G. Smith; Some Observations on the Effect of Inbreeding on Mortality in Kure, Japan—William J. Schull and James V. Neel; Extraneous Variation in Inbreeding Studies—Newton Freire-Maia and J. B. C. Azevedo.

Natural Selection, Readings: Enzyme and Protein Polymorphism in Human Populations—Harry Harris; Metabolic Polymorphisms and the Role of Infectious Diseases in Human Evolution—Arno G. Motulsky; Population Genetics of Haemoglobin Variants, Thalassaemia and Glucose-6-Phosphate Dehydrogenase Deficiency, with Particular Reference to the Malaria Hypothesis—M. Siniscalco, L. Bernini, G. Filippi, B. Latte, P. Meera Khan, S. Piomelli and M. Rattazzi; Sickle-Cell Trait in Human Biological and Cultural Evolution—Stephen L. Wiesenfeld; Patterns of Survival and Reproduction in the United States: Implications for Selection—Dudley Kirk.

The Small Population, Readings: Fisher and Ford on "The Sewall Wright Effect"—Sewall Wright; "Genetic Drift" in an Italian Population—Luigi Luca Cavalli-Sforza; Genetic Effects of Population Size Reduction—Derek F. Roberts; The Distribution of Certain Genes in the Old Order Amish—Victor McKusick, John A. Hostetler, Janice A. Egeland, and Roswell Eldridge; The Development of Inbreeding in an Island Population—Derek F. Roberts; Hopi Indians, Inbreeding, and Albinism—Charles M. Woolf and Frank C. Dukepoo. *Gene Flow*, Readings: Caucasian Genes in American Negroes—T. Edward Reed; Selection, Gene Migration and Polymorphic Stability in a U.S. White and Negro Population—P. L. Workman, B. S. Blumberg and A. J. Cooper.

Genetics and the Future of Man: Eugenics and Utopia—John Maynard Smith.

Il divenire biologico dell'Uomo

By C. Corrain *et al.* 1971. Bologna: Calderini. A vol. in-8°, xvi + 496 pp., 203 figs, index. Bound Lire 6000.

An Italian textbook for university courses in physical anthropology (including a brief chapter on prehistory) by the holder of the Chair of Anthropology at the University of Padua.

Contents

Introduzione. Il rilevamento dei caratteri somatici. Il trattamento statistico della variabilità umana. I fattori della variabilità umana: eredità ed ambiente. Le proporzioni generali del corpo ed il dimorfismo sessuale. La crescita ed il ciclo sessuale. L'interesse comparativo di alcuni caratteri somatici. L'interesse comparativo di alcuni caratteri fisiologici. Le popolazioni umane viventi. Gli altri primati. L'era dell'uomo—Cronologie. Le origini umane.

Lithic Analysis and Cultural Inference: a Paleo-Indian Case

(Anthropological Papers of the University of Arizona, 16).

By E. N. Wilmsen 1970. Tucson: The University of Arizona Press. A vol in-4°, xii + 88 pp, 31 figs, 26 tabs, bibl. Paper \$6.00.

This monograph presents a methodology for analyzing stone artifact inventories within a theoretical framework which attempts to treat archeological data as anthropological evidence—the remains of extinct cultural systems. Data from eight Paleo-Indian sites are utilized to exemplify the method.

Contents

Abstract; Introduction; A Cultural Framework: Cultural Structure, Cultural Variation, Cultural Units; *Archaeological Systematics:* Sampling, Description, Classification; *Procedures:* Site Selection, Sample Selection, Definition of Variables; *The Data:* Sources of Data—Blackwater, Quad, Shoop, Williamson, Lindenmeier, Vernon, Levi, Horner, Denbigh, Big Kiokee Creek; Description of the Data—Material, Striking Platform Characteristics, Flake Angle, The Medial Axis, Artifact Dimensions, Edge Angles, Correlations between Variables, Comparisons between Samples, Tool Categories, Artifact Population Sites; *Processes of Artifact Production:* Raw Material Selection, Technological Variation, Functional Variation; *Site Activities; Structure in Paleo-Indian Culture:* Localization of Paleo-Indian Groups, Social Integration, Subsistence and Task Performance.

Behaviour and Ecology of Nocturnal Prosimians. Field Studies in Gabon and Madagascar

(Advances in Ethology, Supplements to *Journal of Comparative Ethology*, 9). By P. Charles-Dominique & R. D. Martin. 1972. Berlin & Hamburg: Verlag Paul Parey. A vol. in-8°, 92 pp., figs, tabs, bibl., index. Paper DM 39.60.

This small book contains 2 independent reports of field-studies of nocturnal Primate species, one in French and the other in English. Field techniques for studying nocturnal Primates are treated and new perspectives on the zoological relationships between the Prosimians and other Primates are suggested.

Contents

Ecologie et vie sociale de *Galago demidovii* (Fischer 1808; Prosimii): Introduction, Ecologie, Vie sociale, Reproduction; Summary; Zusammenfassung. A Preliminary Field-Study of the Lesser Mouse Lemur *Microcebus murinus* (J. F. Miller 1777): Introduction, The Species Studied, Aims, Methods and Study Areas, Biometric Data, Ecological Characteristics, Distribution Patterns, Vocalisations, Reproduction, Summary, Zusammenfassung.

Man's Ancestors. An Introduction to Primate and Human Evolution

(Introductory Studies in Biology). By I. Tattersall. 1970. London: John Murray. A vol. in-4°, 68 pp., ills, bibl., index. Paper £1.

As an introductory book this concise presentation of palaeoanthropology may prove useful to beginners and other interested readers. The volume is well organized and illustrated.

Contents

Evolutionary processes. Classification. The time-scale of Primate evolution. The order Primates. Human specialisations. Palaeocene and Eocene primates. Oligocene primates. The rise of the pongids. The earliest hominid. The Pleistocene. Late Pliocene and early Pleistocene hominids. Middle Pleistocene hominids. Late Pleistocene hominids. Language and the evolution of the brain.

Economy and Settlement in Neolithic and Early Bronze Age Britain and Europe

Edited by D. D. A. Simpson. 1971. Leicester: Leicester University Press. A vol. in-8°, 188 pp., 177 figs, 8 pls, bibl., index. Cloth £5.00.

Topics in this conference volume comprise: the environment of the third and early second millennia B.C. and man's impact on it; the evidence for the origins of agricultural procedures in northern and temperate Europe; and the human diet which this environment and economy produced.

Contents

Notes on the environment of early farming communities in Britain—J. G. Evans. Habitat change on the calcareous soils of Britain: the impact of Neolithic man—J. G. Evans. Diet, economy and biosocial change in late prehistoric Europe—Don Brothwell. Causewayed enclosures—I. F. Smith. Settlements in late Neolithic Britain—I. J. McInnes. Beaker houses and settlements in Britain—D. D. A. Simpson. Early prehistoric agriculture in Western Europe: some archaeological evidence—P. J. Fowler.

Biochemical Methods in Red Cell Genetics

Edited by J. J. Yunis. 1969. New York & London: Academic Press. A vol. in-8°, xiv + 530 pp., figs, tabs, bibl., index. Bound \$25.00.

This volume covers various aspects of the genetics and metabolism of human erythrocytes with special reference to biochemical methods. The main portion of the book is devoted to red cell enzymes and their relation to genetic variation and disease. Also included is a thorough treatment of hemoglobins. This work would be of special value to research workers, students of genetics, and members of the medical profession who are involved in the field.

Contents

Glucose metabolism in human erythrocytes—Jorge J. Yunis & Walid Yasmineh. Methods for the study of red cell glucose-6-phosphate-dehydrogenase—Arno G. Motulsky & Akira Yoshida. G-6-PD activity of individual erythrocytes and X-chromosomal inactivation—Ernest Beutler. Glutathione—H. K. Prins &

J. A. Loos. 6-Phosphogluconate dehydrogenase and glutathione reductase—George J. Brewer. Pyruvate kinase—Kouichi R. Tanaka. Triosephosphate isomerase deficiency—Arthur S. Schneider. Adenosine triphosphate—George J. Brewer. DPNH-Methemoglobin reductase (diaphorase)—Ernst R. Jaffé. Catalase—Hugo Aebi & Hedi Suter. Galactose-1-phosphate uridyl transferase—Ernest Beutler. The esterases and carbonic anhydrases of human erythrocytes. Richard E. Tashian. Red cell acid phosphatase, phosphoglucomutase, and adenylate kinase—D. A. Hopkinson & Harry Harris. Survey of isozymes of human erythrocytes—George J. Brewer & Charles F. Sing. Human hemoglobins—Titus H. J. Huisman.

The Biopsychology of Development

Edited by E. Tobach, L. R. Aronson & E. Shaw. 1971. New York and London: Academic Press. A vol. in-8°, xx + 596 pp., figs, tabs, bibl., index. Bound \$22.50.

This book analyzes the biopsychology of development on several intra-organismic and phyletic levels of organization, assembling papers from several scientific disciplines. It will be a useful source of information for physiological, comparative, and clinical psychologists, pediatricians, psychiatrists, biologists, zoologists, anthropologists, and animal behaviorists, and will serve as an advanced text for graduate and undergraduate students.

Contents

List of contributors and discussants. List of conference participants. Introduction.

Genetic processes and behavioral development: Differentiation and pattern formation in the development of behavior—Ernest Caspari; Concepts of development—C. H. Waddington.

Neural developmental processes: How a developing brain gets itself properly wired for adaptive function—R. W. Sperry; Development of embryonic motility—Viktor Hamburger; Ontogenesis of sensory function in birds and mammals—Gilbert Gottlieb; Origin and early development of neural elements in the human brain—William F. Windle.

Biochemical processes in behavioral development: Biochemical processes of nervous system development—Williamina A. Himwich; Fetal endocrinology and the effect of hormones on development—Paul Delost; The theory of critical developmental periods and postnatal development of endocrine functions—J. Křeček; Hormonal factors controlling the differentiation, development, and display of copulatory behavior in the Ramstergig and related species—Frank A. Beach; Experiential background for the induction of reproductive behavior patterns by hormones—Daniel S. Lehrman; Effects of environment on development of brain and of behavior—Mark R. Rosenzweig.

Comparative considerations of the development of socialization: Suckling and home orientation in the kitten: A comparative developmental study—Jay S. Rosenblatt; Some problems in the study of the development of social behavior—R. A. Hinde; Diversity in the study of the development of social behavior—C. G. Beer.

Contemporary issues in the study of behavior: Behavioral science, engineering, and poetry—Daniel S. Lehrman; The development of human behavior: theoretical considerations for future research—Dale B. Harris; Levels, categories and methodological assumptions in the study of behavioral development—Herbert G. Birch; Persistent problems in the study of the biopsychology of development—Leon Eisenberg.

Societal implications of the study of behavioral development: Options implicit in developmental styles—Margaret Mead; A behavior analysis of value judgments—B. F. Skinner; In defense of biological freedom—René Dubos.

Introduction to Prehistory. A Systematic Approach

By I. Rouse. 1972. New York: McGraw-Hill Book Co. A vol. in-8°, xviii + 302 pp., 14 figs, 6 tabs, bibl., index. Cloth.

Professor Rouse's important book seeks to introduce the beginning student to the methods and theories of prehistorical research. Prehistory is viewed against a background of all

the natural sciences, which study organic qualities, and of all the social sciences and humanities, which study superorganic qualities. An extensive glossary complements the text.

Contents

Preface.

The nature of prehistory: Prehistory as a historical discipline; Prehistory as a scientific discipline; Prehistory and archeology; Prehistory and ethnography-ethnology; Prehistory and anthropology.

The archeological base: Importance of archeological evidence; Strategy and tactics of archeological research; Development of archeology; The site, its structure and contents; Artifacts; Cultural components and assemblages; Classes, their formation and identification; Classes of cultural remains; Classes versus types of artifacts; Kinds of types; Taxonomic versus typological hierarchies; Classes versus modes of features; Morphological components, assemblages and classes; Exhibition and publication of the remains.

Ethnic classification: Synthetic versus processual strategy; Strategy and tactics of prehistoric research; Systematic units: organic versus superorganic; Peoples versus societies; Development of the study of peoples; Cultural classification; Cultural complexes; Peoples and their cultures; Magnitude of peoples; Dividing peoples; Combining peoples; Hierarchies of cultural units; Co-peoples and co-cultures; Cultural identification; Morphological groups.

Chronological ordering: The chronological approach; Relative and absolute dating; Development of chronological research; Cultural chronologies; Other kinds of chronologies; Distinguishing local area; Establishing local sequences; Synchronizing the sequences; Estimating calendrical dates; Delimiting ages; Converting cultural into ethnic chronologies.

Reconstruction of ethnic systems: The conjunctive approach; Development of conjunctive research; The dimension of form; Settlement patterns; A model of ethnic relationships; The environment; Cultures: activities; Cultures: norms; Cultures: materiel; Cultures: reconstruction; Morphologies: nature; Morphologies: reconstruction; Social structures: institutions; Social structures: interaction; Social structures: norms; Social structures: reconstruction; Languages.

Changes in ethnic systems: Dynamics and explanation; Patterns of change; Processes of change; Systems versus traits; Levels of evolution; Role of norms in superorganic change; Models of macro- and micro-evolution; Lines and traditions; Grades and stages; Centers and climaxes; Development of dynamic research; Processes of change: modification of existing systems; Processes of change: ethnogenesis; Processes of change: revolution; Attitudes toward change; Reductionism.

Conclusion: Summary of prehistorical methods; Relevance of prehistorical research.

The Roots of Civilization. The Cognitive Beginnings of Man's First Art, Symbol and Notation

By A. Marshack. 1972. New York: McGraw-Hill Book Co. A vol. in-4°, 416 pp., ill., bibl., index. Cloth \$17.50.

By examining the artifacts and the cave drawings of the Ice Age, A. Marshack has opened up new pathways to the origins of man's thought, his use of symbol notation and of language. This luxurious and lavishly illustrated book gives a comprehensive account of Marshack's views.

Contents

Notation: The search: The search begins; A bit of bone; The mesolithic bone: Ishango; Tracking the hunter, on paper; Notation: The bones. *Background to the story:* The history of prehistory. An aside. *Notation and art. The research and the ideas:* Notation: Early and late; Time-factored thought; Vault of the sky; The bone of the eagle; Image of the world: Time-factored art; Time-factored death; Sex and the goddess. *The story continued:* The step toward history. *Postscript. Collections of materials examined. Sites and caves on map of ice age Europe.*

Palaeoecology of Africa and of the Surrounding Islands and Antarctica. 5

Edited by E. M. van Zinderen Bakker. 1969. Cape Town: A. A. Balkema. A vol. in-8°, xiv + 242 pp., 56 ills, bibl. Cloth.

This fifth volume of *Palaeoecology of Africa* deals in its entirety with Antarctica in the widest sense and stresses the correlations which exist between the biological and geological history of this region and the southern continents.

Contents

Editorial preface. Foreward. SCAR Sub-Committee on Quaternary Studies. Opening address. Palynological intimations of some pre-Oligocene Antarctic Climates—L. M. Cranwell (Mrs Watson Smith). Investigation of the climatic sequence: a meteorological-empirical approach—H. H. Lamb. The abandonment of the term 'periglacial'—D. L. Linton. Evidence of Pleistocene cryonival phenomena in South Africa—D. L. Linton. Ice age theories and Antarctica—A. T. Wilson. Chemistry and the Quaternary in the Antarctic—A. T. Wilson. The Antarctic ice sheet and the Quaternary history of Antarctica—J. T. Hollin. Climatic record of Late Cenozoic Antarctic ocean sediments related to the record of world climate—J. D. Hays. Données actuelles sur les Archipels des Crozet et des Kerguelen—P. Bellair. Quaternary pollen analytical studies in the southern hemisphere with special reference to the sub-Antarctic—E. M. van Zinderen Bakker, Sr. The terrestrial biogeography of Antarctica—N. M. Wace. Proposals for future Quaternary Studies in the Antarctic—E. M. van Zinderen Bakker, Sr. & M. W. Holdgate.

In the Beginning. An Introduction to Archaeology

By B. M. Fagan. 1972. Boston: Little, Brown & Co. A vol. in-8°, xviii + 366 pp., ills, bibl., index. Bound \$9.50.

This introductory book approaches the subject of archaeology both from the historical angle and from the perspective of the latest scientific methods. Its aim is to provide a comprehensive summary of the methods and techniques of archaeology for beginning students and interested persons. An up-to-date and well produced volume.

Contents

Digging up the past: Introduction; Time; Preservation and discovery; Excavation; Excavation problems. *Analysis of the past*: Environment and subsistence; Technology and artifacts; Ordering and interpretation; Settlement archeology. *Frameworks for the past*: Intellectual frameworks: Mercati to Durkheim; Toward explanation: 1900 to the 1970s; Conclusion. Notes. Bibliography of area archaeologies. Glossary.

Catalogue of Fossil Hominids. 2: Europe

Edited by K. P. Oakley, B. G. Campbell & T. I. Molleson. 1971. London: Trustees of the British Museum (Natural History). A vol. in-8°, xvi + 380 pp., 15 maps, 2 pls, index. Paper £11.50.

This long awaited catalogue is a necessary work of reference for everyone involved in palaeoanthropological research. Asian USSR fossil hominids are included.

Contents

Introduction, Austria, Belgium, British Isles, Bulgaria, Czechoslovakia, Denmark, France, Germany, Gibraltar, Greece, Hungary, Italy, Luxembourg, Malta, Netherlands, Norway, Poland, Portugal, Rumania, Spain, Sweden, Switzerland, Turkey, U.S.S.R., Yugoslavia, Appendix I: Footprints.

Man's Imprint from the Past. Readings in the Methods of Archaeology

(Little, Brown Series in Anthropology). Edited by J. Deetz. 1971. Boston: Little, Brown & Co. A vol. in-8°, xiv + 400 pp., figs, tabs, bibl. Paper \$4.95.

This volume represents an attempt to assemble some fundamental theoretical and methodological papers to give the reader an understanding of recent developments in archaeological method and theory. Both the selection of articles and the lay-out of the book are of a high standard. This reader will be most useful when combined with any of the introductory texts on archaeology.

Contents

Introduction: Must archaeologists dig?—James Deetz.

Archaeology and archaeologists: Archaeology as a career—John Howland Rowe; The dimensions of archaeology—Albert C. Spaulding. *Integrating archaeological material:* Statistical techniques for the discovery of artifact types—Albert C. Spaulding; The type concept revisited—James A. Ford; The use and abuse of taxonomy—John O. Brew; The classification of artifacts in archaeology—Irving Rouse; The type-variety method of ceramic classification as an indicator of cultural phenomena—James C. Gifford; Computers and prehistoric archaeology—George L. Cowgill; The subjective element in archaeological inference—Raymond H. Thompson; Archaeological perspectives—Lewis R. Binford; Problems, methods, and organization: a disparity in the growth of archaeology—Stuart Struever; Late man in North America: archaeology of European Americans—James Deetz; On the interpretation of archaeological evidence in historical and sociological terms—Eóin Macwhite.

Archaeological inference: Archaeology as anthropology—Lewis R. Binford; Analogy in archaeological interpretation—Robert Ascher; Smudge pits and hide smoking: The use of analogy in archaeological reasoning—Lewis R. Binford; Study of the Neolithic social grouping: examples from the New World—Kwang-Chih Chang; A prehistoric community in Eastern Arizona—James N. Hill; Archaeological systems theory and early mesoamerica—Kent V. Flannery; The collapse of Maya civilization in the southern lowlands: a consideration of history and process—Jeremy A. Sabloff & Gordon R. Willey; Archaeological assumptions and ethnographical facts: a cautionary take from New Guinea—Karl G. Heider.

Hunters, Fishers and Farmers of Eastern Europe. 6000–3000 B.C.

By R. Tringham. 1971. London: Hutchinson University Library. A vol. in-8°, 240 pp., 12 pls, 41 figs, bibl., index. Paper £1.50.

This compact book covers the prehistory of Yugoslavia, Bulgaria, Rumania, Hungary, Czechoslovakia, E. Germany and Poland, relating the archaeological material to the prehistory of both central and Western Europe and Western USSR. An important and up-to-date review of both the cultural and the environmental evidence. Drawings are excellent.

Contents

Pronunciation. Preface. Environmental background. Postglacial hunting and gathering communities in eastern Europe. The earliest food-producers 5500-3800 B.C. Economic development and the earliest use of metal c. 3800-3000 B.C. Conclusion.

The Genetics of Human Populations

By L. L. Cavalli-Sforza and W. F. Bodmer. 1971. San Francisco: W. H. Freeman & Co. A vol. in-8°, xvi + 968 pp., 158 figs, 157 tabs, bibl., index. Bound £10.00.

This volume provides a sound introduction to the mathematical techniques which prove useful in the genetics of human populations and in the study of the interactions between human heredity and environment. An excellently produced, comprehensive treatment of this subject, for use by advanced undergraduates and graduate students in physical anthropology, demography, sociology, and related fields.

Contents

Preface. The basic concepts of genetics. Mendelian populations. Deleterious mutations and the estimation of mutation rates. Transient and balanced polymorphisms. Polymorphisms for blood groups, transplantation antigens, and serum proteins: incompatibility selection. Genetic demography and natural selection. Inbreeding. Population structure. Quantitative characters, polygenic inheritance and environmental interactions. The sexual dimorphism. Human evolution. Eugenics, euphenics, and human welfare. *Appendix I*: Statistics and probability. *Appendix II*: Segregation and linkage analysis in human pedigrees and the estimation of gene frequencies. *Appendix III*: Sample problems.

Prehistoric Societies

By G. Clark & S. Piggott. 1970. London: Penguin Books. A vol. in-16°, 352 pp., 95 ills, 8 pls, 4 maps, bibl., index. Paper 50p.

Two leading prehistoric archaeologists jointly present a worldwide outline of man's cultural development from a modern ecological viewpoint. A very readable, well-organized essay.

Contents

Prefatory note. Man's place in nature. The beginnings of culture: Lower Palaeolithic Man. The Middle Palaeolithic. Advanced Palaeolithic hunters and artists. The expansion of human settlement. Hunter-fishers of the recent past and their limitations. Setting the stage for economic change. The origins of farming in the Old and New Worlds: The beginnings of animal domestication and plant cultivation in the Old World. The legacy of agriculture and peasant economies in the New World. Peasant communities of prehistoric Western Asia. The earliest peasant communities of Europe. The later prehistoric settlement of Northern Eurasia and China. Barbarian Europe: The middle phase. Later barbarian Europe and the celtic world.

Not from the Apes

By B. Kurtén. 1972. London: V. Gollancz Ltd. A vol. in-8°, viii + 184 pp., 6 figs, 2 tabs. Cloth £1.75.

Dr Kurtén offers an original interpretation of the phylogeny of hominoid Primates and particularly of "Man". The author's well known style is neat and fluid throughout.

Contents

The record: Man in the petrified zoo; Names; Finding the Dartians; The teeth of superman; Standing up; Rama's ape; Late Tertiary apes; The apes of the Fayum; The forgotten evolution.
The function: The Dartian armory; In the land of the Dartians; The world of Ramapithecus; Beginnings in Africa; The shadow land; The enemy; A way of life in the trees; A way of life on the ground.
Man in the Ice Age: The stage; Enter homo; Neanderthals; Modern man; The alien species; Brains.
Here and now: Selection; The bad genes; Genes and behavior; Death by violence; Chemicals and drugs; Looking forward. Glossary.

Biometeorological Methods

(Environmental Sciences. An Interdisciplinary Monograph Series). By R. E. Munn. 1970. New York and London: Academic Press. A vol. in-8°, xiv + 338 pp., figs, tabs, bibl., index. Bound \$12.50.

This is perhaps the first book to be written about biometeorological methods. It focuses upon the experimental, empirical and physical methods that are most appropriate for each time and space scale. Examples are drawn from the fields of meteorology, hydrology, physiology, ecology, biology, medicine, air pollution, geography, forestry, agronomy and engineering. Human ecologists and all environmental scientists will find this volume useful.

Contents

Preface. Weather and life. Sampling of the atmosphere: Time considerations. Sampling of the atmosphere: Space considerations. The design of biometeorological experiments. Tables, graphs, and charts. Statistical methods I. Statistical methods II: Time series. Physical methods. Physical methods: Illustrative examples. Synoptic applications. Seasonal relationships. Studies of past climates. Climatic classification and indices. Engineering and economic applications. Appendix: Problems.

Women in Between. Female Roles in a Male World: Mount Hagen, New Guinea

(Seminar Studies in Anthropology). By M. Strathern. 1972. London & New York: Seminar Press. A vol. in-8°, xxii + 372 pp., 7 figs, 24 tabs, bibl., index. Bound £4.80.

Dr M. Strathern attempts with this book the first full-length study dealing explicitly with women's status and relations between the sexes in the New Guinea Highlands communities. A tightly documented book, of special interest to social anthropologists either working on New Guinea cultures or on cross-cultural studies of "sex politics" in non-Western societies.

Contents

Notes on orthography and case histories. *Preface:* The case of the good wife. *Part 1. Producers and transactors:* Hagen society; Residence and work: the woman with her husband's kin; The household; The roads of marriage; Kin at her back; Producers and transactors. *Part 2. The independent woman:* Pollution and poison; Marital stability; Focus for blame; Settlement of disputes; Judicial status; Status, incorporation and commitment. *Appendix I:* The subdivision of two Hagen tribes. *Appendix II:* Differences in marriage and divorce patterns between Elti and Kawelka. *Appendix III:* Separation. *Appendix IV:* Exchange marriage. *Appendix V:* Regional differences in bridewealth custom. *Appendix VI:* Composition of bride-wealths. *Appendix VII:* Compensation payments.

Self-Decoration in Mount Hagen

(Art and Society Series). By A. & M. Strathern. 1971. London: G. Duckworth & Co. A vol. in-8°, xii + 208 pp., 115 pls, 6 figs, 7 tabs, bibl., index. Cloth £4.50.

This fine book, co-authored by two distinguished specialists in New Guinea Highlands anthropology, describes the body decoration of the natives in the Mt Hagen area. From examining the aesthetic principles behind the assemblages of ornaments, the general effects that are their aim, and the occasions on which they are worn, the authors suggest just what significance there is in the act of self-decoration and how far it is indeed art.

Contents

Note on orthography. Preface. The setting. Decorations and how they are obtained. Informal and formal decoration. Decoration sets. Face-painting. Reactions to display: the meaning of decorations. The connotations of colour. Self-decoration as art. *Appendix I*: Hagen and other New Guinea societies: a comparative note. *Appendix II*: Items other than the body which receive some decoration. *Appendix III*: Individual variation in head-dresses at the Ndika *moka*, 1967.

Bangwa Funerary Sculpture

(Art and Society Series). By R. Brain & A. Pollock. 1971. London: G. Duckworth & Co. A vol. in-8°, xii + 148 pp., 88 pls, 47 figs, bibl., index. Cloth £4.00.

Bangwa sculpture is a very fine example of the art of the Cameroon grasslands, which has a homogeneity rare even in West Africa. This book deals with the masks and figures owned by the secret societies which perform at the elaborate funerary ceremonies of a member, and contains a first-hand description of a chief's funeral, or cry. A beautifully produced volume.

Contents

Introduction. Bangwa society and culture. Art forms. The artist. The cry-die. Portrait statues, fetishes and Night masks.

House Decoration in Nubia

(Art and Society Series). By M. Wenzel. 1972. London: G. Duckworth & Co. A vol. in-8°, xii + 228 pp., 51 figs, 111 pls, bibl., index. Cloth £5.95.

This volume describes the character and evolution of house decoration in northern Sudanese Nubia, which largely disappeared under the flooding of the Aswan Dam in 1964. The results summarized in this well illustrated book form the only survey made of this highly perishable mud-relief work before its destruction.

Contents

Preface. Introduction. The Nubian people, their homeland and homes. House decoration: Sources of design. Art of the Nubian family. Professional decorators south of Wadi Halfa. Professional decorators north of Wadi Halfa. The iconography of Nubian wall decoration. Aftermath of Nubian wall decoration. Appendix.

Nuba Personal Art

(Art and Society Series). By J. C. Faris. 1972. London: G. Duckworth & Co. A vol. in-8°, x + 130 pp., 80 pls, 15 figs, 10 tabs, bibl., index. Cloth £4.95.

In this fine book Professor Faris documents the unique tradition of art on the person of the south-eastern Nuba, Sudan. Placing it in its social, ecological and cultural setting, the author also specifies the principles of the visual grammar in algorithmic form, using methods derived from generative linguistics.

Contents

Technical note. Preface. Introduction. *Part One—Art in context*: The historical context; The environmental context; The social context; The cultural context; Materials, techniques, anatomies and artists. *Part Two—Design and form*: Designs and the body; The non-representational designs; The representational designs. Conclusions.

New World Prehistory. Archaeology of the American Indian

(Foundations of Modern Anthropology Series). By W. T. Sanders & J. Marino. 1970. Englewood Cliffs: Prentice-Hall, Inc. A book in-8°, viii + 120 pp., 6 figs, index. Paper £1.25.

A clear and up-to-date introductory book on the archaeological evidence of the cultural developments in the New World and its anthropological interpretation. The introduction includes sections on terminology and theoretical considerations.

Contents

Introduction. The New World as a theater of cultural history. Hunting and gathering bands. Agricultural evolution and revolution. Tribes, chiefdoms, and States in mesoamerica. Tribe to Empire in the Central Andes. Marginal tribes and chiefdoms. New World culture history.

Olduvai Gorge. 3: Excavations in Beds I and II, 1960-1963

By M. D. Leakey. 1971. Cambridge: The University Press. A vol. in-4°, xxvi + 306 pp., 121 figs, 10 tabs, 41 pls, bibl., index. Cloth £10.00.

This excellent and long-awaited report by Mary Leakey covers the results of excavations made in Olduvai Beds I and II during years 1960 to 1963. Large quantities of bones and stone tools of early hominids have been recovered from these Lower and Middle Pleistocene formations, in association with abundant and varied environmental evidence. In Part I, attention is devoted to the progress of excavations and the finding of the principal remains, and to the various types of stone and bone artefacts, which the author ascribes to Olduvai, Developed Olduvai, and Acheulean. In Part II the circumstance of the discovery of the hominid skeletal remains are described.

Contents

Foreword by Professor J. D. Clark. Acknowledgements. Map. Introduction. Geologic Background of Beds I and II: Stratigraphic Summary by Professor R. L. Hay. *Part I*: I. Lower Bed I. Site DK and Site FLK NN: Level 4; II. Middle Bed I. Site FLK NN: Levels 1-3. Site FLK: the '*Zinjanthropus*' Level and the Upper Levels; III. Upper Bed I and Lower Bed II. Site FLK North: Levels 1-6, the Clay with root casts and the *Deinotherium* Level. Site HWK East: Levels 1 and 2; IV. The lower part of Middle Bed II. Site HWK East: the Sandy Conglomerate: Levels 3-5. Site FLK North: the Sandy Conglomerate. The Skull Site at MNK; V. The upper part of Middle Bed II. Site EF-HR. The Main Occupation Site at MNK. Sites FC West and FC. Site SHK; VI. Upper Bed II. Sites TK and BK. *Part II*: VII. The discoveries of hominid remains; VIII. Mammalian bones from Beds I and II with evidence of hominid modification; IX. The faunal remains from the living sites in Beds I and II; X. Summary and discussion. *Appendix A*: List of the recorded sites in Olduvai Gorge. *Appendix B*: List of identified faunal remains from known stratigraphic horizons in Beds I and II by Margaret Leakey.

The Archeology of Cape Denbigh

By J. L. Giddings. 1964. Providence: Brown University Press. A vol. in-8°, xvi + 332 pp., 73 pls, 60 figs, 16 tabs, bibl., index. Cloth \$12.50.

A standard work of the first importance to Western Arctic prehistory, published on the occasion of the Centennial Celebration of Brown University. (Received for possible review in May, 1972.)

Contents

Narrative: Field work in 1948; 1949; 1950; 1952. *Nukleet*: Excavations, 1948; 1949; Nukleet collections, 1948; Deposits of Nukleet culture at Iyatayet; The Nukleet culture. *Sites of the Norton culture*: Iyatayet; Madjujuinuk; Gungnuk; Difchahak; The Norton Culture. *The Denbigh flint complex*: Definition of the cultural layer; Techniques; The Denbigh flint culture. *Time and change at Bering Strait*: Dating the Denbigh sequence; Relation to other areas—Cape Prince of Wales, Wales to Cape Espenberg, Trail Creek Caves, Choris Peninsula, Kotzebue, Shesualek, Cape Krusenstern, Battle Rock, Point Hope and Point Barrow, Firth River, Coppermine River, Igloodik and Southampton Island, Greenland and Atlantic, Bristol Bay, Brooks River, Cook Inlet and Kodiak Island, Aleutian Islands, Kobuk River, Brooks Range, Susitna River Valley, Southern Yukon Territory, Great Slave Lake Region, Thelon River, Siberia, Japan. Conclusions. *Appendix I*: The ceramic complexes at Iyatayet by James B. Griffin and Roscoe H. Wilmeth, Jr. *Appendix II*: Skull fragments from Norton levels at Iyatayet by Daris R. Swindler.

The Human Animal. The Mystery of Man's Behavior

By H. Hass. 1970. New York: G. P. Putnam's Sons. A vol. in-8°, 248 pp., ill., bibl., index. Cloth \$6.95.

This book is an attempt to view man's behavioural peculiarity as part of the overall development of the life process. The problem of what parts of our behaviour can be accounted for by our ancestry and may thus be construed as a further development of animal behaviour is investigated. Arguments and pictures are sometimes provocative.

Contents

Point of departure. *Part One—Animal behavior*: Animal and human behavior; Innate behavior patterns; Innate recognition; Instinct and mood; Acquired behavior; And what of Man? *Part Two—Human Behavior*: A voyage of self-exploration; Man and curiosity; Artificial organs; The barometer of the Soul; The friendship signal; Man and order; Gestures; Man and multicellular organism; Imprinting and freedom; Man and society; Man and imagination; The quest for happiness. Epilogue. Appendices.

Valcamonica Symposium

Edited by E. Anati *et al.* 1970. Capo di Ponte: Edizioni del Centro. A vol. in-4°, 584 pp., 259 ills, bibl., index. Bound \$30.00.

This rich symposium volume covers a worldwide presentation of data and interpretations on the subject of prehistoric "art", so to represent a work of reference on this theme. Discussions that occurred at the meeting in 1968 are printed in full after each section of reports.

Contents

Avant-propos. Liste des inscrits au Symposium. Chronique du Symposium (26 illustrations). I—*Introduction*: Parole di apertura—G. Mazzoli; Saluto ai congressisti—P. Ghitti; Saluto della Direzione Generale Antichità e Belle Arti—N. Degrassi; Allocuzione in rappresentanza del Governo—M. Pedini; Discorso inaugurale—P. Graziosi. II—*Peninsule Iberique et France*: Acerca del problema de los origenes del arte levantino—E. Ripoll Perelló; Chronologie de l'art levantin espagnol—P. Bosch-Gimpera; Aportaciones de la "Cueva de Los Grajos" (Cieza, Murcia) al conocimiento del arte rupestre levantino español—A. Beltran; Acerca de la cronologia de la pintura rupestre levantina—A. Beltran; Les pétroglyphes du Bassin Parisien—G. Tassé; Débat sur l'art rupestre de la Péninsule Ibérique et de France—Participants: A. Beltran, E. Ripoll, P. Graziosi, E. Anati, P. Ucko, L. Balout, M. Köbig, R. Batista-Noguera, Jean Abélanet, G. Tassé. III—*Region Alpine et Italie*: Recenti scoperte di incisioni rupestri nelle Valli di Lanzo (Torino)—R. Roggero; Incisioni lineari di Val Fontanalba (M. Bego) raffiguranti statue-stele—M. Rosi; Incisioni rupestri a Carschenna (Canton Grigioni, Svizzera)—C. Zindel; Felsbilder in den Alpenländern Österreichs—E. Burgstaller; Nuove incisioni rupestri del Lago di Garda—M. Pasotti; Un ciottolo inciso del Modenese—B. Benedetti; Débat sur l'art rupestre alpin—Participants: A. Beltran, E. Anati, L. Kaelas, R. Grosso, G. Laeng, M. Mirabella Roberti, F. Rittatore Vonwiller, J. Abélanet, P. Graziosi, H. de Lumley, L. Balout, M. Rosi, Mme. Ciani-Navone, S. Marstrander. IV—*Valcamonica*: L'arte rupestre di Boario Terme-Darfo: Relazione preliminare—E. Anati; Iscrizioni rupestri camune in capitali latine—M. Mirabella Roberti; Essai d'interprétation d'une gravure du Val Camonica—R. Christinger; Il labirinto di Valcamonica e il monumento di Kékénydomb—V. Sümegehy; Su alcuni petroglifi della Valcamonica e della Venezia Tridentina—P. Leonardi; La datazione assoluta delle incisioni rupestri camune: precisazioni—O. Cornaggia Castiglioni; Débat sur la chronologie du Valcamonica—Participants: A. Beltran, E. Anati, O. Cornaggia Castiglioni, F. Rittatore-Vonwiller, A. Broglio, G. Laeng, M. Pasotti, R. Christinger, P. Graziosi. V—*Scandinavie*: A new discovered rock-carving of Bronze Age type in Central Norway—S. Marstrander; Gravures en Kville (Bohuslan): una perçu—A. Fredsjö; Débat sur l'art rupestre scandinave—Participants: P. J. Ucko, A. Fredsjö, B. Almgren, E. Anati, H. Kühn, E. Bostanci, L. Kaelas, C. Doumas, A. Marshack, A. Beltran, S. Marstrander, O. Coisson, F. Rittatore-Vonwiller. VI—*Méditerranée Orientale*: Remarques sur la forme du bateau égéen à l'âge du Bronze ancien—C. Doumas; Nuovi ritrovamenti di Tirisin-Alm—M. Uyanik; Frühe Bukranien in Vorderasien—K. Jaritz; Débat sur l'art de la Méditerranée orientale—Participants: P. J. Ucko, H. Kühn, E. Anati, A. Beltran, M. Uyanik, L. Balout, E. Ripoll, E. Bostanci, P. Graziosi, M. Mirabella Roberti, C. Doumas, K. Jaritz, A. Marshack. VII—*Afrique*: Österreichische Felsbilderaufnahme in Sayala, Ägyptisch-Nubien—K. Kromer; Recenti missioni per lo studio dell'arte rupestre nel Fezzan—P. Graziosi; Proposition d'une chronologie absolue de l'art rupestre du Sahara d'après les fouilles du Tadrart Acacus (Sahara Libyen)—F. Mori; Arte preistorica e struttura, analogia, individualità delle culture—G. Forni; Gravures rupestres inédites du Haut-Atlas—A. Simoneau; Débat sur l'art rupestre du Sahara et de Nubie—Participants: L. Balout, E. Anati, P. Graziosi, K. Kromer, H. Kühn, E. Ripoll, P. J. Ucko. VIII—*Autres Zones*: Réflexions sur les gravures rupestres des Etats Unis—H. Kühn; Sympathetic magic of the hunt as suggested by petroglyphs and pictographs of the Western United States—D. W. Ritter; Pictographs and petroglyphs in Argentina: a preliminary report—C. J. Gradin; El arte rupestre del Parque Nacional Perito Morena (Provincia de Santa Cruz, Patagonia, Republica Argentina)—A. Pedersen; Aspectos da arte pré-histórica no Sul do Brasil—O. Blasi; Débat sur l'art rupestre: autres zones—Participants: E. Ripoll, A. Beltran, S. Marstrander, D. W. Ritter, C. Beretta, L. Balout, E. Anati. IX—*Problemes Generaux*: Aspects mathématiques dans l'art préhistorique—B. A. Frolov; New techniques in the analysis and interpretation of mesolithic notation and symbolic art—A. Marshack; Some aspects of the interpretation of human representations in early post-palaeolithic prehistoric art—P. J. Ucko; The elusive image in La Tène art—J. V. S. Megaw; Etude des incisions rupestres comme manifestation d'un stade d'évolution de l'esprit humain—M. E. P. Koenig; On growth of art—H. F. Blum; Débat sur les problèmes généraux—Participants: L. Balout, P. J. Ucko, P. Graziosi, A. Marshack, E. Anati, K. Kromer, J. Abélanet, A. Beltran, A. Blum. Cloture: Discours de clôture du Symposium—G. B. Scaglia.

Biology and the Human Sciences. The Herbert Spencer Lectures 1970

Edited by J. W. S. Pringle. 1972. Oxford: Oxford University Press at the Clarendon Press. A vol. in-8°, viii + 140 pp., figs, tabs, bibl., index. Bound £2.50. Paper £1.00.

The articles in this book discuss some of the ways in which biology is becoming not only relevant, but vital, to the understanding of human affairs. The book will be of value not only to universities and schools starting the study of the human sciences, but also to sociologists and biologists interested in the wider relevance of their subject.

Contents

Preface—J. W. S. Pringle; Aggression—R. A. Hinde; On controlling population growth—E. Grebenik; Ecology and the evolution of social ethnics—V. C. Wynne-Edwards; Linguistic communication as a biological process—George A. Miller; Race, class and culture—C. D. Darlington; Unique aspects of man's evolution—Theodosius Dobzhansky.

Skin, Heredity, and Malignant Neoplasms

Edited by H. T. Lynch. 1972. Flushing: Medical Examination Publishing Company, Inc. A vol. in-8°, 300 pp., figs, tabs, bibl., index. Cloth Price unknown.

The primary objective of this book is to present a trilogic approach to cancer comprehension and control through the application of the following: (1) physical clues manifested in the skin; (2) genetic information based on the significance of these clues and the family history; (3) diagnostic methods in the search for evidence of cancer. In pursuing this objective the book proves useful in providing insight for the clinician as well as basic fundamental information for the use of the clinical investigator.

Contents

Introduction—Henry T. Lynch; Fundamentals of genetics—Arnold R. Kaplan; Cutaneous clues to internal malignant disease—Harold O. Perry, Joseph M. Kiely & Charles G. Moertel. Tissue culture experiments in hereditary skin cancer: DNA repair synthesis—Vincent M. Riccardi & James E. Cleaver. Xeroderma pigmentosum—Henry T. Lynch. Malignant melanoma—Henry T. Lynch. Ataxia telangiectasia—John F. Jackson. Neurocutaneous diseases—William L. Harlan & Haruo Okazaki. The multiple nevoid basal cell carcinoma syndrome revisited—Robert J. Gorlin & Heddie O. Sedano. Gardner's syndrome—Alvin Watne. The gastrointestinal system, skin, genetics, and cancer—John Woodbury. Immunology, skin, genetics and cancer—Guillermo Villacorte & Robert Townley. Multiple mucosal neuromata syndrome—Neil Schinke. Miscellaneous disorders, genetics, skin, and cancer—Henry T. Lynch. Genetic counseling—Henry T. Lynch. Epilogue—Henry T. Lynch. Appendix: Genetic counseling and cancer genetic units in the United States and other countries of the world—Anne J. Krush.

Animal Memory

Edited by W. K. Honig & P. H. R. James. 1971. New York and London: Academic Press. A vol. in-8°, xiv + 288 pp., figs, tabs, bibl., index. Cloth \$12.

Experimental and theoretical work in the area of animal memory has recently revived. This symposium volume aims at providing a selective survey of current work in this field.

Its relevance for the study of human memory is especially treated in E. Winograd's contribution.

Contents

Forgetting of long-term memories in animals—*Henry Gleitman*. Forgetting as retrieval failure—*Norman E. Spear*. Memory and learning: A sequential viewpoint—*E. J. Capaldi*. The role of interference in association over a delay—*Sam Revusky*. Modification of memory storage processes—*James L. McGaugh & Ronald G. Dawson*. Effects of antibiotics on long-term memory formation in the goldfish—*Bernard W. Agranoff*. Some issues relating animal memory to human memory—*Eugene Winograd*.

From the Hand of Man. Primitive and Preindustrial Technologies

By R. F. G. Spier. 1970. Boston: Houghton Mifflin Co. A vol. in-8°, xii + 164 pp., 58 figs, bibl., index. Paper £1.75.

In this book Professor Spier evaluates some of the varieties of specific technologies created by Man for attaining desirable technical ends. A fresh and readable assessment of the beginnings and growth of the means by which man has controlled and modified his environment. Original, stylized illustrations.

Contents

Foreword—*J. A. Clifton*. Introduction. Technology and culture. Technology and environment. The technological complex. Tools. Materials. Firemaking. Stoneworking. Woodworking. Basketry. Weaving. Pottery. Leather. Metallurgy. Technological change. Summary.

Calibration of Hominoid Evolution. Recent Advances in Isotopic and Other Dating Methods Applicable to the Origin of Man

Edited by W. W. Bishop & J. A. Miller. 1972. Edinburgh: Scottish Academic Press. A vol. in-8°, viii + 488 pp., figs, tabs, bibl., index. Bound £7.50.

This volume contains the texts of nineteen papers presented at a conference entitled *Calibration of Hominoid Evolution*, held under the auspices of the Wenner-Gren Foundation for Anthropological Research at Burg Wartenstein, Austria, in 1971. The conference was originally conceived as a confrontation between "daters" and "consumers" in the field of hominoid evolution. As a result, this book represents an excellent achievement and a standard work.

Contents

Introduction—*W. W. Bishop*. Problems of dating non-woody material from continental environments—*D. L. Thurber*. Age determinations on marine strandlines—*W. S. Broecker & M. L. Bender*. A review of the calibration of deep-sea cores based upon species variation, productivity, and $^{18}\text{O}/^{16}\text{O}$ ratios of planktonic foraminifera—including sedimentation rates and climatic inferences—*O. L. Bandy*. Dating Pliocene and Pleistocene strata using the potassium-argon and argon-40/argon-39 methods—*J. A. Miller*. Selection of suitable material for dating and the assessment of geological error in potassium-argon age determination—*F. J. Fitch*. Geomagnetic reversals—their frequency, their origin and some problems of correlation—*A. Cox*. Potassium-argon dating of geomagnetic reversals and North American glaciations—*G. B. Dalrymple*. Fission track dating: techniques and problems—*R. L. Fleischer & H. R. Hart, Jr.* The dating of fossil bones—*K. K. Turekian & J. L. Bada*. The 'half-life' concept in evolution illustrated from various mammalian

groups—*B. Kurtén*. The dissemination and segregation of early Primates in relation to continental configuration—*A. Walker*. Stratigraphic succession 'versus' calibration in East Africa—*W. W. Bishop*. Radiometric calibration of the European Neogene—*J. A. Van Couvering*. Radiometric dating of sedimentary formations in the lower Omo Valley, Ethiopia—*F. H. Brown*. Further geological studies and potassium-argon dating at Olduvai Gorge and Ngorongoro Crater—*G. H. Curtis & R. L. Hay*. Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution—*H. B. S. Cooke & V. J. Maglio*. Pliocene/Pleistocene Hominidae in eastern Africa—absolute and relative ages—*F. C. Howell*. Evolutionary changes in hominoid dentition through geological time—*D. Pilbeam*. Chronology and the tempo of cultural change during the Pleistocene—*G. Ll. Isaac*. Abstracts, summary of discussions and commentary. *Appendix I*: Three charts showing time relationships of hominoid fossils. *Appendix II*: Sources of dating information and review of methods. *Appendix III*: Notes for conference workshop on palaeomagnetic sampling.

La Préhistoire Ancienne de l'Europe Septentrionale

By J.-L. Baudet. 1971. Paris: Éditions Anthropos. A vol. in-8°, xvi + 260 pp., figs, tabs, bibl., index. Paper Price unknown.

This diligent book covers the evidence on the Lower and Middle Palaeolithic cultures in Atlantic and Northern Europe. A 28-page bibliography on this subject is included.

Contents

Préface—*R. Lantier*. Introduction. *Première partie*: Chronologie Générale; Historique; Données actuelles C 14, K.A.; Hominides; Géochronologie du Nord de l'Europe; Succession typologique; Industries primitives, Ipswichien, Reutélien, Cromérien, Trièdres anciens, Abbevillien I; Abbevillien II; Clactonien; Calaisien; Mesvinien; Levalloisien; Epilevalloisien; Acheuléen et problème de l'Archéologie archaïque. *Deuxième partie*: La zone de rupture entre la péninsule septentrionale et le plateau sous-marin continental nord-européen (Ses analogies stratigraphiques et typologiques terminales avec le Pays de Caux); Région flamando-boulonnaise de Sangatte—Blanc-Nez; Le Calaisien; Wissant villafranchien et pré-historique; Les Varvès marginaux de la plaine flamande; Les Varvès du Pays de Caux; La région de St-Omer; La région des monts de Flandre; Le Dôme du Mélandois; Tectonique et environs de Tournai; Prolongements vers les Pays-Bas et l'Allemagne septentrionale. *Troisième partie*: Notes complémentaires sur les régions classiques d'Allemagne, Belgique, Hollande et Nord de la France; Le Weimarien; son origine sa répartition, rapports avec le Levallois V; Le Mesvinien, son gisement principal (car. Hélin, Spiennes); Le Levalloisien IV du Hainaut belge; Le Clactonien belge; L'Epilevalloisien du N.E. (de l'Escaut à l'Eifel); L'Epilevalloisien de la crête de partage Sambre—Escaut (plateau de St-Quentin *sensu lato*); L'axe Scarpe—Haine; L'Acheuléen de l'Artois; Canchy en Ponthieu. *Quatrième partie*: Problèmes du Paléolithique baltique; Historique; Le Calaisien baltique (Hohwacht, Jammerland); L'Altschleimünde; Le biface du Himmerland; Les os brisés d'Hollerup; Samsø; Les fouilles et découvertes Madsen dans l'Isefjord, Sjaelland (Abbevillien II, Clactoniens, Acheuléen). Perspectives et conclusions.

Comparative Methods in Sociology. Essays on Trends and Applications

Edited by I. Vallier. 1971. Berkeley, Los Angeles, London: University of California Press. A vol. in-8°, viii + 478 pp., figs, tabs, bibl., index. Cloth £6.55.

The essays in this volume are intended to help social scientists to do better comparative research and thereby to improve our possibilities for creating more satisfactory explanations or theories. These broad aims are advanced throughout the book by consideration of (i) early strategies of comparison, (ii) general theory and comparative research, (iii) systematic procedures and applications.

Contents

Comparative studies: A review with some projections—*David E. Apter*. Alexis de Tocqueville as comparative analyst—*Neil J. Smelser*. The methodology of Marx's comparative analysis of modes of production—*R. Stephen Warner*. Max Weber's comparative approach and historical typology—*Guenther Roth*. Comparative studies and evolutionary change—*Talcott Parsons*. Frameworks for comparative research: Structural anthropology and the theory of action—*Guy E. Swanson*. Empirical comparisons of social structure: Leads and lags—*Ivan Vallier*. Intelligible comparisons—*Morris Zelditch, Jr.* Cross-national survey research: The problem of credibility—*Sidney Verba*. Applications of an expanded survey research model to comparative institutional studies—*Robert H. Somers*. Comparative studies: A selective, annotated bibliography—*Susan Bettelheim Garfin*.

Anthropological Research. The Structure of Inquiry

By P. J. Pelto. 1970. New York, Evanston, London: Harper & Row. A vol. in-8°, xiv + 370 pp., ill., figs, tabs, bibl., index. Cloth.

Well written and well produced, this book will prove stimulating for all professional researchers in cultural anthropology.

Contents

Preface. Introduction: Elements of research methodology; Assessing the usefulness of definitions; Inductive and deductive approaches; Theory, method, and empiricism. *Science and anthropology:* Science and history; Science and controlled experiments; The problem of cross-cultural comparisons; Science: A definition; Anthropology and problems of methodology; Conclusions. *Operationalism in anthropological research:* Operationalism and intersubjectivity; operationalism and operationism; Operationalism in anthropology; Theory vs reality: The operational compromise; Summary and conclusions. *Units of observation: Emic and etic approaches:* The emic or "new ethnography" approach; The eticists; Emic, etic, and the goals of anthropology; The emic-etic compromise—"imbedded emicism". *Tools of research:* Participant observation; Key-informant interviewing; Collection of life histories; Structured interviews; Questionnaires; Ratings and rankings; The semantic differential technique; Projective techniques; other psychological research instruments; Unobtrusive measures; Technical equipment in field work; Multi-instrument research. *Counting and sampling:* Examples of counting in ethnographic reports; Problems of representativeness: sampling; Patterning and sampling; Summary and conclusions. *Measurement, scales, and statistics:* Murdock, social structure, and the chi-square test; Types of measurements: nominal, ordinal, interval, and ratio scales; Tests of independence and measures of association; Parametric and nonparametric statistics; More complicated statistical operations; Tests of independence do not prove causation; The Meehl paradox: some problems in hypothesis testing; Specialized competence in statistics. *Art and science in field work:* Strategies in the art of field work; Hazards and punishments of field work; Sources of tension in field work; Elements of community study; Description and hypothesis testing; Multicommunity research projects; Assistants; Communication among fieldworkers; Team research at special events; Interdisciplinary research; Summary. *Building anthropological theory: Methods of comparative research:* Statistical cross-cultural comparisons; Causal inferences from correlational data; Small sample studies, controlled comparisons; and "natural experiments"; Multiple hypotheses: the strategic elimination of alternatives; Methodology and the culture of anthropology. *Epilogue. Relevance, ethics, and the future of anthropology. Appendices:* Appendix A—Notes on research design; Appendix B—The Guttman scale: a special type of ordinal measure; Appendix C—On using computers; Appendix D—Field guide to North American celebrations.

The Archaeology of Ancient Egypt

(Bodley Head Archaeology). By T. G. H. James. 1972. London, Sydney, Toronto: The Bodley Head. A vol. in-8°, 144 pp., ill., bibl., index. Bound £1.95.

This richly illustrated book is an up-to-date introduction to our knowledge of Egyptian civilization and to its archaeological discovery.

Contents

Preface. The outline of Egyptian history. The beginnings of real archaeology. Discovering pyramids. A triumph of painstaking archaeology. A great man and his estate. The expulsion of the Hyksos. A golden burial. Makers of the house of eternity. The problems of Tanis. The sacred bulls of Memphis. The decipherment of hieroglyphs. The silver treasures of Barbarians. Postscript.

Environment and Archeology. An Ecological Approach to Prehistory

By K. W. Butzer. 1971. London: Methuen & Co. Ltd.
2nd ed. A vol. in-8°, xxviii + 704 pp., 95 figs, 23 tabs,
bibl., index. Bound £8.00.

First published in 1964, K. Butzer's well known textbook has been revised and expanded and now includes three new chapters dealing with North American and Australian topics. This new edition confirms the high standard of the previous and has an even wider appeal.

Contents

Foreword to the Second Edition. Foreword to the First Edition. *Part I. Introduction:* Prehistoric environment, geography, and ecology; Stratigraphy; Dating and absolute chronology. *Part II. Vegetation, soils, and geomorphology as environmental indices:* The zonal concept; Vegetation and climate; Soil processes and soil types; Glacial and periglacial geomorphology; Humid, arid, and tropical geomorphology; Mammalian and human distributions. *Part III. Interpretation of Pleistocene sediments:* Field and laboratory study of sediments; Stream and lake sediments; Wind-borne and slope sediments; Cave sediments; Coastal phenomena and sea level fluctuations; Geomorphological study of archeological sites. *Part IV. Contributions of the biological sciences:* Palynology and paleobotany; Paleontology and paleotemperatures. *Part V. Some Pleistocene environments of the old and new world:* Mid-latitude Europe during the Late Pleistocene; The Mediterranean region during the Late Pleistocene; Some African environments of the Late Pleistocene; Late Pleistocene environments of North America; Some paleoclimatic problems of the interglacials; The climatic changes of the Pleistocene. *Part VI. Man-land relationships in prehistory:* Early subsistence and settlement patterns; Human origins in sub-saharan Africa; Man-land relationships of Acheulian hunter-gatherers; The European mousterians and their environment; Upper Paleolithic man-land relationships in Europe; The Paleo-Indians; Origins and man-land relationships; Early colonization of Australia; Environmental change and cultural adaptation in early postglacial Europe; Agricultural origins in the Near East as a geographical problem; Agricultural dispersals into Europe and Northern Africa; Agricultural settlement and urban origins in the Near Eastern floodplains.

Introducing Archaeology

(Bodley Head Archaeology). By M. Magnusson. 1972.
London, Sydney, Toronto: The Bodley Head. A vol.
in-8°, 128 pp., ill., bibl., index. Bound £1.95.

In this illustrated book, the editor of the *Bodley Head Archaeologies* series tells the story of both classical and contemporary archaeology.

Contents

What is archaeology? The early history of archaeology: The first 'archaeologists', The English antiquarians, Early excavations, The first time-scale. *The heroic age of archaeology:* Giovanni Battista Belzoni, Heinrich Schliemann, Sir Austen Henry Layard, Lord Elgin, Jean-François Champollion, Edward Thompson. *Archaeology comes of age:* The first dating techniques, General Pitt Rivers, Sir Arthur Evans, Sir Flinders Petrie, Sir Leonard Woolley. *The twentieth century (1):* The discovery of Machu Picchu, The tomb of Tutankhamun, Scythian excavations, The Sutton Hoo ship. *The twentieth-century (2):* The civilisation of the Indus Valley, The search for Camelot, Industrial archaeology, Underwater archaeology, The palace at Fishbourne, The temples at Abu Simbel. *Science in archaeology. Illicit archaeology. Amateur archaeology.*

Acta Bernensia. 6: Die Gliederung der Schnurkeramischen Kultur in der Schweiz

By C. Strahm. 1971. Bern: Verlag Stämpfli & Cie AG.
A vol. in-4°, 196 pp., ill., tabs, bibl., Cloth SFr.80.

The Swiss Corded Ware Group, representing the most South Westerly off-shoot of the Corded Ware Culture Province, affords considerable insight into the way of life of this period. The Swiss material is mainly from settlements—lake dwelling sites—and, due to the fine preservation, is particularly rich and important. This study is thorough, accurate, and well presented.

Contents

Vorwort. Einleitung. Alfgabe; Vorgehen; Quellenlage; Forschungsgeschichte. Erster teil: Utoquai—Einleitung: Ausgrabungen; Lage und Ausdehnung des Dorfes; Schichtaufbau; Baureste; Stratigraphie. Funde: Allgemeines; Funde aus der unteren Schicht; Funde aus der oberen Schicht: Gefäße, Waffen und Werkzeuge, Schmuck; Fundkatalog: Fundübersicht, Katalog—Gefäße, Waffen und Werkzeuge, Schmuck. Auswertung: Gefäße; Waffen und Werkzeuge; Schmuck. Schluss. Zweiter teil: Sutz—Einleitung. Die keramischen funde: Beschreibung; Katalog. Auswertung. Dritter teil: Schöfflisdorf—Einleitung. Grabbau: Grabformen; Zusammenstellung der Angaben nach den Grabungsberichten und Fundkatalog. Fundbeschreibung: Keramik; Kleinfunde. Auswertung. Vierter teil: Ergebnisse—Kritik des Einheitshorizontes. Die schweizerische Schnurkeramik und der Einheitshorizont. Die Stufe Sutz. Die stufe schöfflisdorf. Die stufe utoquai. Die stratigraphische stellung der schweizerischen Schnurkeramik. Die chronologische Stellung der schweizerischen Schnurkeramik. Die schweizerische Schnurkeramik und die frühe Bronzezeit. Zusammenfassung; French, English, and Russian summaries.

Aboriginal Man and Environment in Australia

Edited by D. J. Mulvaney & J. Golson. 1971. Canberra: Australian National University Press. A vol. in-8°, xxii + 390 pp., 31 pls, 59 figs, 39 tabs, bibl., index. Cloth \$12.50.

This book is the outcome of a series of seminars by scholars in many fields who have brought to bear the skills of many disciplines in interpreting a vast array of challenging new information. It will appeal not only to scholars but to all who have an interest in the history of the Australian environment and the story of first human settlement. A very well produced volume.

Contents

Preface. Sea level changes and land links—J. N. Jennings. Evidence for late quaternary climates—R. W. Galloway. Vegetation, soils, and climate in late quaternary Southeastern Australia—A. B. Costin. River systems and climatic changes in Southeastern Australia—Simon Pels. Pleistocene Salinities and climatic change: Evidence from lakes and lunettes in Southeastern Australia—J. M. Bowler. The Australian arid zone as a prehistoric environment—J. A. Mabbutt. Man, fauna and climate in Aboriginal Australia—J. H. Calaby. Cave sediments as palaeoenvironmental indicators, and the sedimentary sequence in Koonalda Cave—R. Frank. The archaeology of Koonalda Cave—R. V. S. Wright. Coastal aborigines of Southeastern Australia—R. J. Lampert. Prehistory in the Cape York Peninsula—R. V. S. Wright. Man and environment in Northwest Arnhem Land—Carmel White. Prehistoric research in Timor—I. C. Glover. New Guinea and Australian Prehistory: the 'Neolithic Problem'—J. Peter White. Australian aboriginal food plants: some ecological and culture-historical implications—Jack Golson. Open sites and the ethnographic approach to the archaeology of hunter-gatherers—Nicolas Peterson. Habitat and economy: A historical perspective—Roger Lawrence. Arid region aborigines: The Pintubi—J. P. M. Long. The demography of hunters and farmers in Tasmania—Rhys Jones. Changes in the aboriginal population of Victoria 1863–1966—Diane E. Barwick. The racial affinities and origins of the Australian aborigines—A. G. Thorne. Genetic evidence and its implications for aboriginal prehistory—R. L. Kirk. Linguistic evidence and

aboriginal origins—D. T. Tryon. Art and aboriginal prehistory—Robert Edwards. Aboriginal social evolution: A retrospective view—D. J. Mulvaney. Appendices: Species list of the food plants of Arnhem Land, Cape York, and Central Australia; Generic list of the food plants of Arnhem Land, Cape York, and Central Australia; Genera and species recorded as food sources in Malaysia, present but apparently unused in Australia.

The Cultural Context of Learning and Thinking. An Exploration in Experimental Anthropology

By M. Cole, J. Gay, J. A. Glick & D. W. Sharp. 1971.
London: Methuen & Co. A vol. in-8°, xx + 306 pp.,
ills, bibl., index. Cloth £3.50.

From the in-depth study of the thinking processes of members of a Kpelle tribal group in West Africa, a general contribution to the relation between culture and cognitive development is presented. This book (produced in association with T. Ciborowski, F. Frankel, J. Kellemu & D. F. Lancy) represents a new and interesting cross-cultural approach to this set of topics.

Contents

Culture and thinking. An unorthodox ethnography. Classification. Classification, learning, and memory. Classification and learning of physical attributes. Culture, logic, and thinking. Conclusions. *Appendix A*: A description of the major subclasses of the *Set* chart. *Appendix B*: The application of the similarity-distribution technique. *Appendix C*: Free association. *Appendix D*: Additional data from similarity-mediation study. *Appendix E*: Details of free-recall experimental procedures and results of standard experiments. *Appendix F*: Technical aspects of the conduct of cross-cultural memory research. *Appendix G*: Recall of items presented in a story context. *Appendix H*: Stimulus matching as a measure of classification. *Appendix I*: Rule learning. *Appendix J*: Procedural details and instructions for initial inference experiment. *Appendix K*: Details of final inference experiment.

New Perspectives in Archeology

Edited by S. R. Bindford & L. R. Bindford. 1968.
Chicago: Aldine Publishing Co. 3rd printing, 1970.
A vol. in-8°, x + 374 pp., figs, tabs, bibl., index. Cloth
\$7.50.

This book outlines the viewpoint of recent American archaeologists who are working to change the direction and focus of the discipline, in order to achieve its stated aims: the reconstruction of cultural history, the reconstruction of lifeways and the delineation of cultural processes. The editors and authors must be congratulated for having brought together this important set of contributions.

Contents

Archeological theory and method: Archeological perspectives—Lewis R. Binford. Explanation in archeology—Albert C. Spaulding. The inference of residence and descent rules from archeological data—James Deetz. Variability and change in the Near Eastern Mousterian of Levallois facies—Sally R. Binford. Method and theory of Upper Paleolithic archeology in Southwestern France—James R. Sackett. *Investigating variability in the archeological record: A single occupation unit*: Some aspects of prehistoric society in East-Central Arizona—William A. Longacre. Broken K Pueblo: Patterns of form and function—James N. Hill. Computer analysis of archeological data from Teotihuacan, Mexico—George L. Cowgill. Archeological lessons from an Apache Wickiup—William A. Longacre and James E. Ayres. Establishing cultural heterogeneities in settlement patterns: An ethnographic example—Bobby Jo Williams. *Investigating variability in the*

archeological record: Variability among occupation units: Value systems and trade cycles of the late archaic in the Midwest—Howard D. Winters. Investigations of late prehistoric social organization in New York State—Robert Whallon, Jr. Evidence of social organization from Western Iran, 8000–4000 B.C.—Frank Hole. Social and economic systems in formative Mesoamerica—Kent V. Flannery and Michael D. Coe. Woodland subsistence-settlement systems in the lower Illinois valley—Stuart Struever. Post-Pleistocene adaptations—Lewis R. Binford. *Discussion*—Comments by Richard B. Lee, Irven DeVore, Morton Fried, Edward P. Dozier, David F. Aberle and Marvin Harris.

Peasants in Cities: Readings in the Anthropology of Urbanization

Edited by W. Mangin. 1970. Boston: Houghton Mifflin Co. A vol. in-8°, xl + 216 pp., figs, tabs, bibl. Paper £2.00.

In this set of readings, an authority on “urban anthropology” brings together a variety of anthropological statements on the transformation of life styles as rural peoples take up residence in the cities of the world. Involved problems of anthropological responsibility are stressed by the editor in his introductory essay.

Contents

Foreword—J. A. Clifton. Preface. Introduction. Barriers and channels for housing development in modernizing countries—John C. Turner. Similarities and differences between two types of Peruvian communities—William Mangin. Behind the back of the city: “Provincial” life in Lima, Peru—Paul L. Doughty. Urbanization case history in Peru—William Mangin. Tales from the Barriadas—William Mangin. The ritual dimension of rural-urban networks: The fiesta system in the northern highlands of Bolivia—Hans C. Buechler. Rio’s Favelas: The rural slum within the city—Frank Bonilla. Urban relocation and family adaptation in Puerto Rico: A case study in urban ethnography—Roy Simón Bryce-Laporte. A study of the urbanization process among Mixtec migrants from Tilantongo in Mexico City—Douglas S. Butterworth. Morocco’s expanding towns—Hassan Awad. Medan: The role of kinship in an Indonesian City—Edward M. Bruner. Kishan Babu—Joseph Lelyveld. Some preliminary observations concerning the anthropology of industrialization—Harold A. Gould. Urban migration and the residence of children in Kampala—Aidan Southall. Africans in industrial towns in Northern Rhodesia—J. Clyde Mitchell. Nigerians: The dream is unfulfilled—Leonard Plotnicov. Onitsha market literature—Donatus I. Nwoga.

Man, Settlement and Urbanism

Edited by P. J. Ucko, R. Tringham & G. W. Dimbleby. 1972. London: G. Duckworth & Co Ltd. A vol. in-8° xxviii + 980 pp., figs, tabs, pls, bibl., index. Cloth £18.00.

A sensible edition of the papers delivered at an international meeting of the Research Seminar in Archaeology and Related Subjects held at the Institute of Archaeology, London, in December 1970.

Contents

Preface. Introduction—R. Tringham.

Part one: Non-urban settlement. (Section one: Concepts, in theory and practice.) *B. W. Blouet*: Factors influencing the evolution of settlement patterns; *D. A. Davidson*: Terrain adjustment and prehistoric communities; *K. V. Flannery*: The origins of the village as a settlement type in Mesoamerica and the Near East: a comparative study; *P. Gathercole*: The study of settlement patterns in Polynesia; *M. R. Jarman*, *C. Vita-Finzi* & *E. S. Higgs*: Site catchment analysis in archaeology; *R. S. MacNeish*: The evolution of community patterns in Tehuacán Valley of Mexico and speculations about the cultural processes; *I. Rouse*:

Settlement patterns in archaeology; *C. C. Taylor*: The study of settlement patterns in pre-Saxon Britain. (Section two: The influence of mobility on non-urban settlement.) *B. Allchin*: Hunters or pastoral nomads? Late Stone Age settlements in Western and Central India; *S. Bökönyi*: Zoological evidence for seasonal or permanent occupation of prehistoric settlements; *J. D. Clark*: Mobility and settlement patterns in sub-Saharan Africa: a comparison of late prehistoric hunter-gatherers and early agricultural occupation units; *J. D. Clark*: Palaeolithic butchery practices; *I. C. Glover*: Settlements and mobility among the hunter-gatherers of south-east Asia; *G. Ll. Isaac*: Comparative studies of Pleistocene site locations in East Africa; *R. B. Lee*: Work effort, group structure and land-use in contemporary hunter-gatherers; *P. Simonson*: The transition from food-gathering to pastoralism in north Scandinavia and its impact on settlement patterns; *J. C. Woodburn*: Ecology, nomadic movement and the composition of the local group among hunters and gatherers: an East African example and its implications; *J. J. Wymer & R. Singer*: Middle Stone Age occupational settlements on the Tzitzikama coast, eastern Cape Province, South Africa. (Section three: The influence of ecology and agriculture on non-urban settlement.) *W. Allan*: Ecology, techniques and settlement patterns; *C. Doumas*: Early Bronze Age settlement patterns in the Cyclades. *D. French*: Settlement distribution in the Konya Plain, south-central Turkey; *J. R. Harlan*: Crops that extend the range of agricultural settlement; *D. R. Harris*: Swidden systems and settlement; *V. M. Masson*: Prehistoric settlement patterns in Soviet central Asia; *J. Mellaart*: Anatolian Neolithic settlement patterns; *J. Middleton*: Patterns of settlement in Zanzibar; *P. Mortenson*: Seasonal camps and early villages in the Zagros; *J. Oates*: Prehistoric settlement patterns in Mesopotamia; *B. Reynolds*: Kwandu settlement: isolation, integration and mobility among a south-central African people; *B. Soudský & I. Pavlů*: The Linear Pottery Culture settlement patterns of central Europe; *W. Watson*: Neolithic settlement in East Asia.

Part two: Factors influencing both non-urban and urban settlement. (Section one: Population, disease and demography.) *R. Boyd*: Urbanisation, morbidity and mortality; *D. Brothwell*: Community health as a factor in urban cultural evolution; *A. Forge*: Normative factors in the settlement size of Neolithic cultivators (New Guinea); *R. Layton*: Settlement and community; *C. Renfrew*: Patterns of population growth in the prehistoric Aegean; *V. Reynolds*: Ethology of urban life; *P. E. L. Smith*: Land-use, settlement patterns and subsistence agriculture: a demographic perspective. (Section two: Territoriality and the demarcation of land.) *R. D. Martin*: Concepts of human territoriality; *M. J. Rowlands*: Defence: a factor in the organization of settlements; *R. Tringham*: Territorial demarcation of prehistoric settlements; *W. A. West*: The effect of private and public law on the use and development of land. (Section three: Techniques, planning and cultural change.) *B. A. L. Cranstone*: Environment and choice in dwelling and settlement: an ethnographical survey; *G. Danisman*: The architectural development of settlements in Anatolia; *M. Douglas*: Symbolic orders in the use of domestic space; *H. W. M. Hodges*: Domestic building materials and ancient settlements; *J. G. Hurst*: The changing medieval village in England; *A. Ritchie*: Inferences from settlements in Britain in the first millennium B.C.; *F. W. Schwerdfeger*: Urban settlement patterns in northern Nigeria (Hausaland).

Part three: Urban settlement. (Section one: Development and characteristics of urbanism.) *D. Grove*: The function and future of urban centres; *M. G. Smith*: Complexity, size and urbanization; *B. G. Trigger*: Determinants of urban growth in pre-industrial societies; *P. Wheatley*: The concept of urbanism. (Section two: Regional and local evidence for urban settlement.) *A. M. Ali*: Meroitic settlement of the Butana (central Sudan); *D. M. Dixon*: The disposal of certain personal, household and town waste in ancient Egypt; *B. J. Kemp*: Fortified towns in Nubia; *B. J. Kemp*: Temple and town in ancient Egypt; *D. O'Connor*: The geography of settlement in ancient Egypt; *J. D. Ray*: The House of Osorapis; *H. S. Smith*: Society and settlement in ancient Egypt; *E. Uphill*: The concept of the Egyptian palace as a "ruling machine"; *R. McC. Adams*: Patterns of urbanization in early southern Mesopotamia; *K. Branigan*: Minoan settlements in east Crete; *H. E. W. Crawford*: Stimuli towards urbanization in south Mesopotamia; *S. C. Humphreys*: Town and country in ancient Greece; *G. A. Johnson*: A test of the utility of Central Place Theory in archaeology; *A. McNicoll*: The development of urban defences in Hellenistic Asia Minor; *H. J. Nissen*: The city wall of Uruk; *D. Oates*: The development of Assyrian towns and cities; *P. J. Parr*: Settlement patterns and urban planning in the ancient Levant: the nature of the evidence; *J. N. Postgate*: The role of the temple in the Mesopotamian secular community; *T. C. Young, Jr.*: Population densities and early Mesopotamia urbanism; *J. Alexander*: The beginnings of urban life in Europe; *K. Branigan*: Verulamium and the Chiltern villas; *M. W. C. Hassall*: Roman urbanization in western Europe; *D. Sturdy*: Correlation of evidence of medieval urban communities; *J. B. Ward-Perkins*: Central authority and patterns of rural settlement; *P. Morton-Williams*: Some factors in the location, growth and survival of towns in West Africa; *W. G. L. Randles*: Pre-colonial urbanization in Africa south of the Equator; *A. Whitty*: Zimbabwe and Inyanga; *G. H. A. Bankes*: Settlement patterns in the lower Moche Valley, north Peru, with special reference to the Early Horizon and Early Intermediate Period; *W. Bray*: Land-use, settlement patterns and politics in prehispanic Middle America: a review; *K. C. Day*: Urban planning at Chan Chan, Peru; *D. J. Robinson*: Changing settlement patterns in colonial Hispanic America. Conclusion—*S. Piggott*.

The Evolution of Urban Society. Early Mesopotamia and Prehispanic Mexico

By R. McC. Adams. 1966. Chicago: Aldine Publishing Co. A vol. in-8°, xii + 196 pp., 4 figs, bibl., index. Cloth \$7.50. Paper \$2.95.

This comparative analysis, stemmed from a series of lectures delivered at the University of Rochester in 1965, is concerned with the presentation and analysis of regularities in our two best-documented examples of early, independent emergence of urban societies. Essential similarities in the evolutionary patterns of early Mesopotamia and Prehispanic Mexico are identified.

Contents

The problem and the evidence. Subsistence and settlement. Kin and class. Parish and polity. Conclusion.

Fundamental Properties of the Human Nervous System

(Monographs in Psychology.) By V. D. Nebylitsyn. 1972. New York, London: Plenum Press. A vol. in-8°, viii + 336 pp., figs, tabs, bibl., index. Cloth Price unknown.

This volume fully describes the experimental studies of the physiological bases of the properties of the nervous system accomplished in different Russian laboratories. The book covers basic principles in the study of the structure of fundamental properties of the nervous system, experimental indices of dynamism of nervous processes, and the relationship of orienting reactions to basic properties of the nervous system.

Contents

Preface. Basic principles of approach to the study of properties of the nervous system. Structure of the basic properties of the nervous system. Experimental indices of dynamism of nervous processes. Orienting reactions and their relationship to basic properties of the nervous system. Dynamism of the nervous system as reflected in some EEG indices. Dynamism of excitation and its EEG correlates in children. Referent indices of strength of the nervous system. Strength of the nervous system and absolute sensitivity. The role of the strength of the nervous system in the organism's reactions to stimuli of increasing intensity. Mobility of the nervous processes and its indices. The nature of balance of the nervous properties according to the basic properties of the nervous system. The problem of partial characteristics in the measurements of nervous system properties.

The Ontogeny of Vertebrate Behavior

Edited by H. Moltz. 1971. New York & London: Academic Press. A vol. in-8°, xii + 500 pp., figs, tabs, bibl., index. Cloth \$22.50.

This book presents important new research on the question of how species' typical behavior patterns come to be organized during the life history of an animal. The vertebrates included are birds, rodents, lagomorphs, monkeys, and Man. The book will be of value to all those with an interest in behavior development, including psychologists, ethologists, endocrinologists, and behavioral biologists.

Contents

Preface. The study of behavioral development—*D. S. Lehrman & J. S. Rosenblatt*. The development of visual perceptual systems—*Maurice Hershenson*. Early experience and problem-solving behavior—*Barton Meyers*. The ontogeny of emotional behavior—*Douglas K. Candland*. Ontogeny of play and exploratory behaviors: A definition of problems and a search for new conceptual solutions—*W. I. Welker*. The ontogeny of sexuality—*Richard E. Whalen*. The ontogeny of maternal behavior in some selected mammalian species—*Howard Moltz*. The ontogeny of mother-infant relations in Macaques—*Leonard A. Rosenblum*. Imprinting—*P. P. G. Bateson*. Vocal learning in birds—*Peter Marler and Paul Mundinger*. The ontogeny of language—*Joseph Church*.

Introduction to the Study of Animal Populations

By G. Andrewartha. 1970. London: Chapman & Hall Ltd. 2nd ed. A vol. in-8°, xiv + 286 pp., figs, tabs, bibl., index. Paper £2.50.

In this book Professor Andrewartha considers how environment affects an animal's existence with regard to survival and reproduction, thus influencing the distribution and abundance of the population to which the animal belongs. The environment, for the purpose of this analysis, is divided into five well-defined components. At each step the theoretical considerations are illustrated by reference to ecological case histories, the emphasis throughout being on behavioural adaptations to environment as well as on evolutionary history. This second edition has been widely revised.

Contents

Preface to Second Edition. Preface to First Edition. Part I: Theory: *The history and scope of ecology*—Introduction, Population ecology: the study of the distribution and abundance of animals, The broad bases for population ecology, How to write about ecology, further reading; *Environment*—Introduction, The idea that environment is divisible into five components, Further reading; *Components of environment; resources*—Introduction, Relative shortages, Absolute shortages, The distribution and abundance of resources; *Components of environment; mates*—Introduction, Shortage of mates, The prevalence of sparseness, Adaptations that increase the chance of finding a mate when numbers are few; *Components of environment; predators and pathogens; aggressors*—Introduction, Predators, Pathogens, Aggressors; *Components of environment; weather*—Introduction, Temperature, Moisture, Light; *Components of environment; malentities*—Introduction, Browning's definition of hazards, Malentities; *Components of environment; more about the ecological web*—Introduction, Some advantages in being one of many, Interactions in the ecological web may be important, Interactions in the ecological web may ramify, Ecological barriers as part of the ecological web; *Theory; the numbers of animals in natural populations*—Introduction, The conditions of 'commonness' and 'rareness' in local populations, The conditions of 'commonness' or 'rareness' in natural populations. Part II: Practical course: *Methods for estimating density, patterns of distribution and dispersal in populations of animals*—Introduction, The measurement of relative density, The measurement of absolute density, The measurement of 'aggregation' in natural populations, Dispersal, Glass experiments on the estimation of density, distribution and dispersal; *Physiological responses to temperature*—The influence of temperature on speed of development, The lethal influence of extreme temperature; *Behaviour in relation to moisture and food*—Moisture, Food. Appendix.

Developmental Studies on Giant Chromosomes

(Results and Problems in Cell Differentiation, 4). Edited by W. Beermann. 1972. Berlin, Heidelberg, New York: Springer-Verlag. A vol. in-8°, xvi + 228 pp., figs, tabs, bibl. Cloth.

Giant polytene chromosomes have been for decades a favoured subject of studies centring upon the involvement of individual chromosomal sub-units in the process of cell differentiation. Without striving for completeness, the editor and the contributors to this book

make an effort to render a thorough and up-to-date picture of the situation in their particular field, and on this basis to discuss all possible angles of general biological interest. The volume is dedicated to the memory of Jack Schultz.

Contents

Chromomeres and genes—*Wolfgang Beerman*. Chromosomes isolated from unfixed salivary glands of *Chironomus*—*Markus Lezzi & Michel Robert*. Replication in polytene chromosomes—*George T. Rudkin*. Transcription in giant chromosomal puffs—*Claus Pelling*. Puffing patterns in *Drosophila melanogaster* and related species—*Michael Ashburner*. Relation of puffing to bristle and footpad differentiation in *Calliphora* and *Sarcophaga*—*Dieter Ribbert*. The control of puffing in *Drosophila hydei*—*Hans D. Berendes*. Balbiani ring activities in *Acricotopus lucidus*—*Reinhard Panitz*.

Archaic Roman Religion

By G. Dumézil. 1970. Chicago & London: The University of Chicago Press. 2 vols in-8°, xxxvi + 716 pp., index. Cloth £11.25.

This is the first of Georges Dumézil's books to appear in English. The translation (by P. Krapp) has been revised and annotated by the author. This important essay will be of value to all those scholars involved in anthropological studies of myth, religion and ritual

Contents

Foreword, by Mircea Eliade. Preface. *Preliminary remarks*—Uncertainty of the history of the first centuries; Political history and religious history; The most ancient Roman religion: *Numen* or *Deus*? Characteristics of the Roman gods; The lost mythology: The example of the *Matralia*; From mythology to history; The Indo-European heritage at Rome; Conservatism of Roman religion: The case of the *Iugis auspicium*; The value of formulary evidence; The Roman scholars; The so-called pontifical revolution; Some characteristics of Roman religion; Balances in Roman religion; The vocabulary of the sacred; The purpose of this book. *First Part: The great gods of the archaic triad*—The archaic triad: the documents; Interpretation: the three functions—Jupiter, Mars, Quirinus; The archaic triad: Complements. *Second part: Ancient theology*—The capitoline triad—Capitoline Jupiter, Juno, Minerva, The capitoline triad; The fires of public worship; Frameworks—The beginnings, The times, The places; Man—The living, The dead; Forces and elements—Third function, second and first functions. *Third part: Extensions and mutations*—Personified abstractions; The gods of the neighbors; The gods of the enemy; The gods of the merchants; The first Greek gods; An attempt at chronology; Religion during the second Punic war; The first literary evidence; Ideological innovations; Thrusts and resistances; The civil wars and religion. *Fourth part: The Cult—Sacra publica; Sacerdotes; Signa and Portenta*; Notes on the private cults. *Appendix: The religion of the Etruscans*—Introduction; The "Libri" of the Etruscans, *Libri fulgurales*; *Libri haruspicini*; *Libri rituales*; The gods; Groupings of gods; The world of the dead; Selected works on Etruscan religion.

Red Man's America. A History of Indians in the United States

By R. M. Underhill. 1971. Chicago & London: The University of Chicago Press. 2nd ed. A vol. in-8°, x + 398 pp., 53 pls, 11 maps, bibl., index. Cloth £3.75, paper £1.80.

This is the revised and improved edition of Ruth Underhill's well known book, first published in 1953.

Contents

The red man discovers America: The first migrations and the peopling of the two continents. America blooms: The earliest corn-growers and the high cultures of nuclear America. Civilized tribes: The five important tribes of the Southeast who were later moved to Oklahoma. Encirclement: Pressure of whites in the Southeast and removal of Indians. They have gone: Algonkian tribes of the Atlantic seaboard. A woodland league of nations: The five tribes of the Iroquois. People of the calumet: tribes of the Great Lakes and Upper Mississippi. The new rich of the plains: Early residents of the Buffalo country and others who moved in with the coming of the horse. The peaceful corn-growers: Southwestern agriculturists: The Mogollon, Hohokam, Pueblo, and Pimans. Late arrivals: The Navaho and Apache. Those who had little to lose: Tribes of the Great Basin and the Plateau. West coast medley: Indians of California. The potlatch-givers: Tribes of the Pacific Northwest from Northern California to the Canadian Border. Protective uncle: Measures taken by the Government on the Indian's behalf.

Évolution et Techniques. 1: L'homme et la Matière

By A. Leroi-Gourhan. 1971. Paris: Éditions Albin Michel. 2nd ed. A vol. in-16°, 352 pp., 577 figs, Paper Price unknown.

A new and expanded edition of the book in which Professor Leroi-Gourhan summarizes his ideas on simple technology and cultural evolution. The second volume is forthcoming.

Contents

Introduction. *Structure technique des sociétés humaines*: Tendances et fait, Degrés du fait, Hiérarchie des techniques. *Moyens élémentaires d'action sur la matière*: Les percussions, Le feu, L'eau, L'air, La force. *Les transports*: Portage humain, Portage animal, Trainage et roulage, Traction et direction, Navigation, Voies de communication. *Les techniques de fabrication*: Solides stables, Solides fibreux, Solides plastiques, Solides souples, Fluides. *Premiers éléments d'évolution technique*: La technologie comparée. Légendes des figures.



Obituary Notice

Gerhard Heberer✠

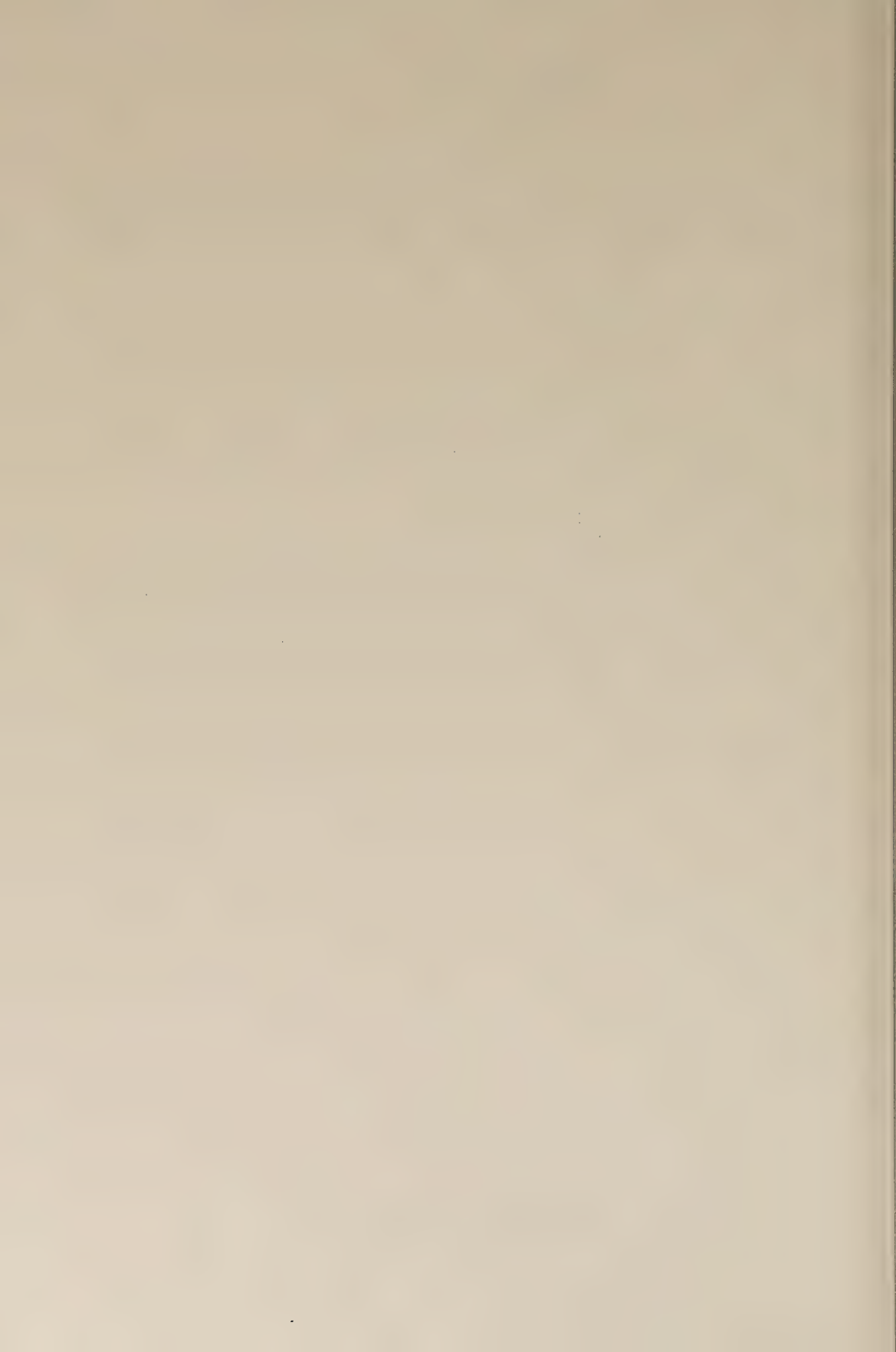
Gerhard Heberer, the well-known German palaeoanthropologist and scientist of evolution, died in Göttingen on 13 April 1973, shortly after celebrating his 72nd birthday. His name was known throughout the world, mainly through his work as editor and co-author of the standard volumes *Evolution der Organismen*, shortly to be completed in its third printing.

G. Heberer was born on 20 March 1901 in Halle/Saale, Germany. He studied zoology, comparative anatomy, anthropology and archaeology in Halle/Saale and received his doctorate with a dissertation on cytogenetics in 1924 under the auspices of Valentin Haecker. From 1927–1928 he participated as an anthropologist and zoologist in a German expedition to the Sunda Islands. Following this, he received an assistantship at the Department of Zoology at the University of Tübingen and in 1938 became professor for “Anthropogenetik” at the University of Jena. After the end of the Second World War, he moved in 1947 to Göttingen, building up, in connection with the Department of Zoology, the “Anthropologische Forschungsstelle”, which encompasses an excellent and comprehensive palaeoanthropological collection.

The scientific works of G. Heberer in anthropology are concentrated for the most part on the comprehensive study of human evolution and fossil Man, especially the Australopithecines. Most notable among these are his articles contained in the *Evolution der Organismen* (2nd printing, 1953), *Menschliche Abstammungslehre* (1964) and in *Hundert Jahre Evolutionsforschung* (1960), as well as his work *Fossilgeschichte der Hominoiden*, in *Primatologia* (1956). Due to Heberer's ability to present his material in a manner intelligible to the general public, his publications concerning human evolution also became popular among laymen.

With the death of Gerhard Heberer, German palaeoanthropology has lost one of its greatest mentors.

C. Vogel
Göttingen



Verle E. Headings

*Medical Genetics Unit, Howard
University College of Medicine,
Washington, D.C., U.S.A.*

Received 6 September 1972

Mechanisms of Gene Product Diversification in Primate Carbonic Anhydrases*

Genetic and phylogenetic variation in the Primate carbonic anhydrases reflects at least four categories of gene product diversification; gene duplication, variation in quantity of gene product, conformational isozymes, and amino acid substitutions corresponding to single point mutations. Such a degree of diversity within this Primate protein system offers an unusual opportunity to investigate mechanisms of gene action, genome organization, and relationships between enzyme structure and function.

1. Introduction

A systematic description of both the categories of variability and the characteristics of the individual variants of Primate carbonic anhydrases can serve several purposes. Because of its liberal diversity of variation this system is a potentially valuable model for investigating genome organization and gene action in Primates. In recent years the hypothesis of non-adaptive evolution has been presented to account for the fact that a large proportion of genetic loci are polymorphic, as well as for the apparent equivalence of many amino acid substitutions (Kimura, 1968; King & Jukes, 1969; Boyer *et al.*, 1969). According to this hypothesis, the majority of carbonic anhydrase variants may in fact be functionally trivial. However, the relatively large number and diversity of variants in this system offers unusual opportunity to evaluate the significance of associated functional variation.

In this paper I will synthesize the available information on the categories of qualitative and quantitative variability in the Primate carbonic anhydrases. The genetic bases as well as the known functional equivalents of these variants will be reviewed. Some proposals for future research directed toward identifying additional functional variation will also be mentioned.

Primate carbonic anhydrase lends itself admirably to genetic studies. It is a single polypeptide molecule of about 265 amino acid residues and contains one zinc atom. It is reasonably abundant in red cells of most Primates. At least one physiologic function has been characterized in great detail. The principal function appears to be the reversible hydration of carbon dioxide ($\text{CO}_2 + \text{H}_2\text{O} \leftrightarrow \text{H}_2\text{CO}_3$), which is required for transport and elimination of this metabolite and for regulating hydrogen ion concentration in secretions of various organs. The enzyme is functionally versatile as shown by its ability to cleave ester bonds in a series of non-physiologic substrates (Tashian, 1969a). A large amount of genetic and phylogenetic diversity has been identified.

At least six categories of gene product modification have been documented among various protein systems: gene duplication with subsequent independent function and evolution of the duplicated products; complex formation between identical gene

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products, products of duplicated genes, or diverse gene products; variation in quantity of gene product; conformational interchange between multiple forms of a single gene product; reduction of polypeptide structure by cleavage; amino acid substitutions, additions or deletions in gene product reflecting single point mutations.

2. Categories of Variation in Carbonic Anhydrase

Four of the above categories have been identified among the carbonic anhydrases of Primate red blood cells and were initially detected by a variation in electrophoretic pattern. The multiple electrophoretic forms of the enzyme, which reflect multiple molecular forms, are collectively designated as isozymes. Two nomenclature systems for these isozymes occur in the literature, one reflecting genetic differences and the other denoting biochemical distinctions. The genetically informative nomenclature system is used throughout this paper.

Gene duplication

A duplicated gene with subsequent independent evolution of the two gene products (CA I and CA II) with respect to amino acid sequences, relative quantities in a given tissue, and specific enzyme activities is evident in Primate carbonic anhydrases (Nyman, Strid & Westermarck, 1968; Tashian, Shreffler & Shows, 1968). The CA II/CA I hydrazase activity ratio for the human red cell isozymes is 30 under approximately physiological assay conditions (Gibbons & Edsall, 1963). In human red cells CA I and CA II are differentially responsive to humoral changes associated with hyperthyroidism; quantity of CA I is reduced by $\frac{2}{3}$ while CA II is relatively unaffected (Headings & Tashian, 1970a). Further search for differences between these isozymes at an environment interaction level is clearly indicated.

Modification of structure by mutation

A relatively large number of inherited variants reflect structural modifications in the enzyme. In Man electrophoretic variants in CA I are all rare in the populations in which they have been described, with the possible exception of the CA I_c variant (Carter, Tashian, Huntsman & Sacker, 1972). Only one CA II variant has been identified so far in Man and this occurs in polymorphic frequency in the American Black population (Moore, Funakoshi & Deutsch, 1971). Seven variants of human CA I have been reported and single amino acid substitutions have been identified at five different sites in the molecule (cf. Carter *et al.*, 1972). Each substitution is consistent with single base-pair changes. In some species, as in the macaques, a number of electrophoretic variants occur in polymorphic frequencies (gene frequency of 1% or greater) at both the CA I and CA II loci (Tashian, Goodman, Headings, De Simone & Ward, 1971). In the above examples pedigree data have shown the variants to be inherited traits. The identified electrophoretic variants among the apes and those monkeys for which pedigree data has not been collected (Tashian *et al.*, 1968; Tashian, 1965) are assumed by analogy to be inherited traits.

The functional equivalents of the intraspecies variants are only partially evaluated. As shown in Table 1, among six variants of human red cell CA I, only one is associated

Table 1

Relative hydrazase activity of human CA I electrophoretic variants

CA I variant	*Relative hydrazase activity	Reference
CA I _a (usual)	1.00	—
CA I _b Michigan	0.42	Tashian (1969a)
CA I _c Guam	1.04	Tashian, Riggs & Yu (1966)
CA I _d Michigan	0.86	Shows (1967)
CA P Mut	1.00	Funakoshi & Deutsch (1970)
CA I _e Portsmouth	0.98	Carter <i>et al.</i> (1972)
CA I _e Hull	0.98	Carter <i>et al.</i> (1972)

* Specific hydrazase activity was compared relative to the usual or wild type form, CA I_a.

with major modification of specific CO₂ hydrazase activity. The specific esterase activity of this same variant toward β -naphthyl acetate is enhanced by increasing the concentration of zinc in solution with the enzyme (Tashian, 1969b). At least three of the human CA I variants when present in heterozygous state occur in a quantitative ratio of about one-third that of the wild type allele product (cf. Tashian, 1969a). Among the gibbons a particular variant, occurring in polymorphic frequency, contains immunochemical cross-reacting material without evidence of esterase activity on stained electrophoretic pattern (Tashian, 1969a). This suggests a structural modification which impairs the catalytic function of the molecule.

Functional changes in red cell CA I are evident when comparing a variety of species for hydrazase and esterase specific activities (Tashian *et al.*, 1968; Tashian, Douglas & Yu, 1964). Such functional variation is presumably dictated by interspecies differences in amino acid sequence of the enzyme. This conclusion is reinforced by the observation that specific activity of CA II is relatively invariant among Primates, possibly reflecting the smaller interspecies variation in amino acid composition. In the pig-tailed macaques three variants of CA I (a, b, c) with differing electrophoretic mobilities are each associated with characteristic quantities of enzyme as measured by a sensitive radioimmunoassay (De Simone, Magid & Tashian, 1973a). The mechanism of the effect on quantity of enzyme by these presumed modifications in enzyme structure is under investigation. Two alternative hypotheses are differential limitation on rate of synthesis and differential stability of the enzyme.

Modification of quantity by mutation

Studies on deficiencies of carbonic anhydrase in Primates have yielded evidence for inherited quantitative variation which appears to be dissociated from enzyme structure. An inherited variant creating a 5000-fold decrease in red cell CA I and a $\frac{2}{3}$ decrease in CA II in the homozygous state (Headings & Tashian, 1971a) occurs at a frequency of 0.33 among pig-tailed macaques (Tashian *et al.*, 1971). The following findings are consistent with the hypothesis of a mutation in a site which affects the structure of neither CA I nor CA II but which differentially modifies the quantities of these products: the inheritance pattern is that of either an allele at the CA I locus or a gene tightly linked to it (Tashian *et al.*, 1971); the measured biochemical and immunochemical properties of the deficient enzyme are indistinguishable from the non-deficient enzyme

(Headings & Tashian, 1971a); both CA I and CA II are affected by this mutant and in the individual who is heterozygous intermediate quantities of CA I and CA II are observed (De Simone *et al.*, 1973a; Headings & Tashian, 1971a); the mutant appears to be differentially expressed among various tissues (Headings & Tashian, 1971a); the mutant is associated with at least three different electrophoretic variants of CA I (De Simone *et al.*, 1973a); studies on *in vitro* synthesis of carbonic anhydrase suggest that the effect of the mutant on quantity of CA II occurs in a cis but not in a trans relationship (De Simone *et al.*, 1973b).

The physiological significance of this deficiency is not at this point fully evaluated. There are no apparent clinical manifestations in affected individuals. The total enzyme activity (CA I and CA II) in the red cells of such individuals has been calculated to be 34% of that in non-deficient individuals (Headings & Tashian, 1971a). Data from earlier detailed studies on *in vivo* inhibition of carbonic anhydrase in a variety of non-Primate species suggested that the physiological requirements for hydrase activity are about 1000 fold less than what is available under normal circumstances (cf. Maren, 1963).

Recently tentative evidence was obtained for a second deficiency variant of CA in the pig-tailed macaque which is associated with approximately a 10-fold greater deficiency in CA I as well as additional deficiency in CA II in comparison to the initially described variant (Headings & Tashian, unpublished data).

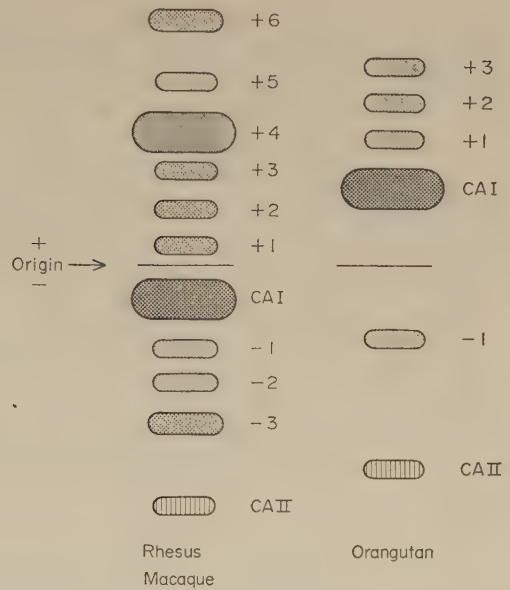
Measurement on quantity of CA I in red cells taken repetitively from a small sample of human subjects revealed a persistent two fold range among individuals (Headings & Tashian, 1970b). The mechanism of this variability has yet to be investigated. Quantitative differences among species and genuses have not been studied in detail, however, gross inspection of protein stain intensity on starch gel electrophoretic patterns does verify that there is indeed a large range of variability.

Conformational isozymes

Conformational isozymes represent a major category of variability in primate carbonic anhydrase (Headings & Tashian, 1971b). In studies on CA I from red cells of rhesus macaque where a large number of electrophoretic forms are easily detected (at least 10) it was shown that an interconversion of forms occurs in such a manner that forms migrating toward the anode and cathode arise from a single given form. Furthermore the isolated minor electrophoretic forms convert more readily toward the mobility position of the major form. Earlier data obtained on human CA I and CA I (+1), a minor electrophoretic form, showed that they do not significantly differ from one another in specific CO₂ hydrase activity, tryptic peptide pattern, amino acid composition and immunochemical specificity (Fine, Boffa, Charrel, Laurent & Derrien, 1963; Derrien & Laurent, 1969). Tertiary configuration, specifically two-dimensional axis ratio, differs significantly (Derrien & Laurent, 1969). Supportive observations on reversible changes in tertiary conformation have been presented for several other proteins (Kitto, Wasserman & Kaplan, 1966; Epstein & Schechter, 1968; Kaplan, 1968).

Multiple electrophoretic forms of human CA I were generated under relatively harsh conditions such as pH 12-13 (Laurent & Derrien, 1969; Funakoshi & Deutsch, 1969). Forms generated from a single given form were shown to migrate in one direction only in the electrophoretic field and these were interpreted in one report (Funakoshi & Deutsch, 1969) as arising from successive deamination of CA I. Unpublished data

Figure 1. Diagram of starch gel esterase zymogram of chloroform-ethanol extract of hemolysates partially purified on a DEAE-cellulose column. Degree of shading for major and minor forms of CA I approximates relative staining intensities. Electrophoresis and staining procedures were as described by Tashian (1969a).



indicates that interconversion of human CA I isozymes also occurs without treatment by excessively alkaline pH. The conversion from a single isolated form to forms which migrate toward both the anode and cathode, as shown for the rhesus macaque CA I, is not easily interpreted by a deamination hypothesis.

Marked species differences occur in the capacity of CA I to develop conformational isomers. Differences in three properties of the electrophoretic conformational patterns are evident on an interspecies comparison of stained starch gel patterns for rhesus macaque and orangutan red cell CA I (Figure 1): number of isozymes; relative mobilities of the isozymes one to another; relative proportions distributed among the isozymes. Preliminary data indicate that the red cell CA I of capuchin monkey and of bush-baby possess markedly less capacity for conformational isozymes than do the species illustrated in Figure 1. Among rhesus and Japanese macaques a particular electrophoretic variant consists of an essentially equal distribution, of what appears to be a single allele product, between two forms of differing mobilities (Tashian *et al.*, 1971).

Preliminary and projected studies on conformational variation in CA I include a variety of interspecies comparisons of relative distribution of enzyme among conformers, relative specific hydrazase and esterase activities of intraspecies conformers, and comparison of amino acid sequences in Primate CA I's of widely divergent propensity to conformational interchange. This latter approach may identify constellations of amino acids which correlate with capacity to form conformational isozymes.

3. Significance of Variation

A key question in any attempts to correlate change in structure with change in enzyme activity involves a possibility that a particular structural change has prime significance for a seemingly minor or unidentified function. The extensive information on the physiology of carbonic anhydrase in many vertebrate and non-vertebrate organisms points to a role in CO_2 transport in the blood, and an ultimate influence on hydrogen ion

concentration in certain organ secretions and other body fluids (Maren, 1967). From studies on carbonic anhydrase of turtle urinary bladder mucosal cells, evidence has been presented to suggest that the enzyme may play a role in active transmembrane transport of chloride ion (Scott, Yousif & Brodsky, 1970).

Further investigation of functional equivalents of structural variation must include a measure of *in situ* distribution within the cell of both CA I and CA II, structurally modified gene products, and conformational isozymes. Preliminary evidence on differential association of CA I and CA II with subcellular structures in dog kidney cells suggests that CA II may be preferentially associated with intracellular membranes (Wistrand & Rao, 1968).

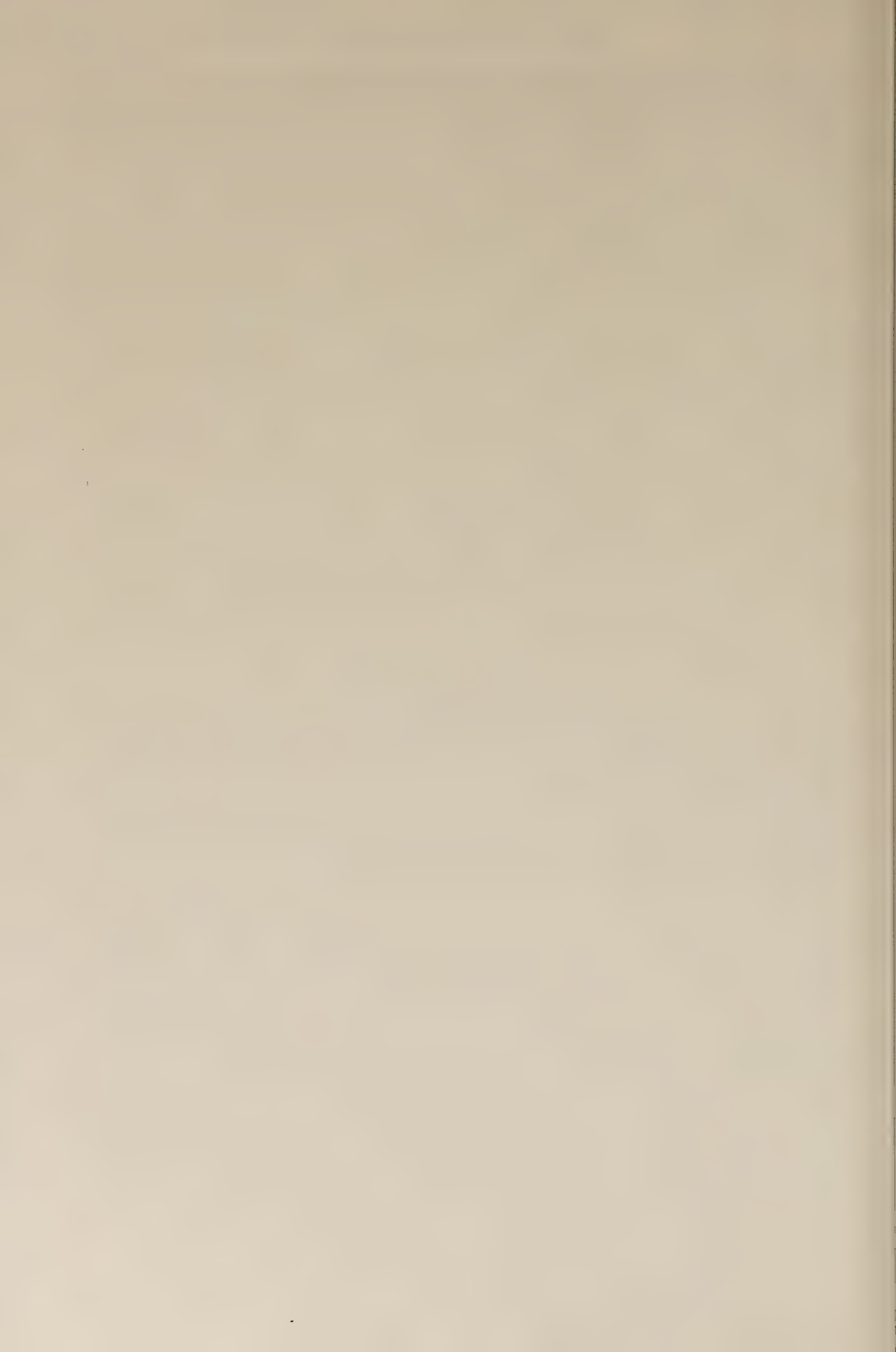
The relative distribution of isozymes among tissues is potentially of functional significance. The relative amounts of CA I and CA II differ among tissues of the pig-tailed macaque (Headings & Tashian, 1971a). In this study the effects of a deficiency variant also appeared to be differentially expressed among tissues. Unreported observations in comparative tissue studies also point to the possibility of more than two genetic loci for this enzyme.

Genetic and phylogenetic variation in primate carbonic anhydrases has provided information on genetic mechanisms of quantitative variation and relationships between change in structure of gene product and either specific activity or quantity of the product. Clearly, more detailed studies on a variety of tissues are necessary in order to reasonably evaluate the functional significance, in clinical or adaptive terms, of a given qualitative or quantitative variant. The recent development of new sensitive techniques will facilitate this inquiry.

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Patricia A. Snyder

Department of Psychology,
Bucknell University,
Lewisburg, Pa., U.S.A.

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Behavior of *Leontopithecus rosalia* (Golden-lion Marmoset) and Related Species: A Review*

Perhaps the most interesting behavior exhibited by marmosets is the formation of permanent pair bonds and the resultant equal dominance of both the male and the female in the family situation. Behavior patterns are stereotyped and it is relatively simple to establish daily behavioral repertoires for the different species. Scent marking behavior is an effective means of sexual and social communication. Its full significance to sexual behavior is yet to be known. Other forms of communication include tactile, visual and acoustic signalling. Fraternal, chimeric twinning is common in marmosets. The marmoset father assumes responsibility for carrying and caring for the infants, when the mother decides to relinquish the infants to him. After that time, she receives the infants only to feed them. A typical day for a *L. rosalia* family might include the following: (1) The activity begins at dawn; (2) The marmosets forage and exercise; (3) The animals sun and groom themselves and each other at the tops of trees; (4) The family moves to the lower branches of the trees and rests during the warmest part of the day; (5) The marmosets forage and play in the early afternoon; (6) The animals take short rests and forage until sundown; and (7) The marmoset family beds down together, when the sun sets.

Very little is known concerning the social and sexual behaviors of the New World monkey *L. rosalia* in its natural habitat. In order to ensure the perpetuation of this endangered species, more must be learned about its behavior patterns and reproductive physiology. These studies can be made most easily in captive situations at the present time. Because breeding problems exist in captivity for this species, the number of animals available for study is limited. The reason or reasons causing breeding failure between captive born mates is not defined. The following aspects of *L. rosalia* behavior and physiology must be reconsidered and studied more closely in order to solve the existing breeding difficulties: the maturation, growth and social development, in infants; the length of the estrus cycle and its behavioral correlates; the formation of pair bonds; the production of pheromones; and the onset and offset of pregnancy.

1. Introduction

Few detailed accounts exist describing the social and sexual behaviors of the New World Primate species, *Leontopithecus rosalia*, the Golden-lion marmoset. The majority of reports that have been published are descriptions of the marmoset's behavior in captive circumstances and the limitations imposed on this animal by an artificial environment must be realized. A study of the Golden-lion marmoset in its natural habitat is limited by the animal's small size, rapid movement, lack of noticeable sexual dimorphism, and geographical location. Much of what is known about this primate has been inferred and generalized from information concerning other members of the marmoset family, Callithricidae.

Leontopithecus rosalia is severely threatened by extinction in its natural and artificial

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habitats. In their natural environment vast deforestation for the sugar cane and lumber industries, housing developments, pressure of native hunters and a planned bridge over a strategic bay make their distribution practically a suburb of the city of Rio de Janeiro (Coimbra-Filho, 1970b). Originally, the Golden-lion marmoset was distributed along a strip of coastal forest approximately 500×100 km within the states of Espirito Santo and Rio de Janeiro. Today, *L. rosalia* occupies a 900 km^2 area along the lower Sao Joao River in the state of Rio de Janeiro (Bridgewater, 1972). Population density decrease has followed the decrease in land area. In 1966, the American Association of Zoological Parks and Aquariums Subcommittee on Primate Conservation blacklisted *L. rosalia* and subsequently the Wild Animal Propagation Trust established a committee on the Golden-lion marmoset. In 1967, the Brazilian Fauna Protection Law No. 5.197 was passed and regulated the exportation of animals from Brazil (Bridgewater, 1972). It is important that we learn all we can about the particular sexual and social patterns of behavior of the Golden-lion marmoset in order to ensure its perpetuation. The following is a general introductory summary of observed marmoset behavior in captive and feral environments.

2. Group Relations

In general, marmosets organize into family units consisting of an adult male and female, the new-born infants, and two juveniles and/or one or two young adults. This family unit is observed in most captive species and is presumed to be a similar organization as that established by marmosets in the feral state (Fitzgerald, 1935; Lucas, Hume & Smith, 1937; Hill, 1957; Epplé, 1967a, b, 1970a; DuMond, personal communication; personal observation, 1971*). Family life generally is serene, with little quarreling among group members (Lucas *et al.*, 1937; Epplé, 1967b, 1970b). Conflicts arise when the group is disorganized or when a strange conspecific is introduced into the group; i.e. any interference with the establishing or the already established hierarchical family unit results in conflict (Epplé, 1967b). Fights between two animals of the opposite sex never have been observed to occur within the established family unit (Fitzgerald, 1935; Epplé, 1967b, 1970b; personal observation, 1971).

(i) Behavior interactions among adult males in the organized group

In most marmoset species an observable dominance hierarchy is established (Fitzgerald, 1935; Epplé, 1967b). In captive circumstances the adult male father is dominant over any other adult and juvenile males in the family group. If the male is placed in a cage with non-family adult males, dominance position is established through fighting (Epplé, 1967b). It has been reported that only dominant males will mate with the dominant females. The dominant male in the group more frequently displays genital presentations, scent marking activity, attacking and fighting than the subordinate males (Epplé, 1967b, 1970b; personal observation, 1971).

(ii) Behavior interactions among adult females in the organized group

The adult female mother is dominant over all other adult and juvenile females within the family unit (Fitzgerald, 1935; Epplé, 1967b; personal observation, 1971). In an

* All personal observations, 1971, were made and recorded in the months of January, March and September at Monkey Jungle in Goulds, Florida.

established family unit only the adult female mother will become pregnant. In an unorganized group situation, usually only the dominant females become pregnant, although the inferior females have been seen to copulate with fertile males (Epple, 1967*b*, 1970*a*). The dominant female also tends to display genital presentations, scent markings activity, attacking and fighting more often than the inferior females (Epple, 1970*b*).

(iii) *Relation of the dominant male to the dominant female*

This relationship is thought to be a stable, monogamous arrangement with no overt aggressive interactions displayed between the two individuals (Fitzgerald, 1935; Epple, 1967*b*; Moynihan, 1970). Epple (1967*b*) and Coimbra-Filho (1969) believe that there is a tendency for the alpha pair to inhibit all other mating within the family group. How this inhibition of mating occurs, or even the certainty of the inhibition is not known. Both the dominant male and the dominant female play important roles in the defense of their home range territory (Epple, 1970*a*; personal observation, 1971).

Just before and just after parturition in *L. rosalia* the female assumes a more dominant position within the family unit (personal observation, 1971). She displays more aggressive patterns of behavior and directs them toward other members of the family. Immediately following parturition and for a period of one or two days, the male is not allowed near the female and infants. Any attempts made by the male to approach the female results in attacks and growls made by the female and directed toward the male. The female becomes particularly aggressive during feeding periods. At this time she vocalizes in a disturbed manner and attacks other family members who appear to want to eat mealworm and crickets. The other family members tolerate her behavior and never retaliate.

(iv) *Relation of the adult male to the young*

The dominant male in most marmoset family units carries the newly born infants during the first few weeks of their life, surrendering them to the female only during nursing periods (Fitzgerald, 1935; Lucas *et al.*, 1937; Hill, 1957; Crandall, 1964; Epple, 1967*b*; Moynihan, 1970). Lorenz (personal communication, 1972) speculates that the period of time which the infants are carried by the mother depends on the physical health of the female. If the mother is weak after giving birth, then she allows the male to carry the infants almost immediately following parturition. If the female is stronger, she carries the infants for a longer period of time. In one instance, a successful breeding female (*L. rosalia*) carried her infants for approximately seven days after parturition before she allowed the male to carry them. Then she allowed the male to carry them for only a few hours a day until about the ninth day after parturition when the male carried the infants almost continuously except for the nursing periods (personal observation, 1971). In another instance, a *L. rosalia* female allowed the male to carry the infants only two days after parturition. This breeding pair was a newly formed pair and this birth episode was their first together (personal observation, 1971).

The male generally tolerates the presence of juvenile animals in the family group. Although the dominant male may drive out the young male adults in the group, he is concerned particularly with the newly born, washing them at birth and caring for, carrying and grooming the neonates until they become physically independent (Fitzgerald, 1935; Epple, 1967*b*).

(v) *Relation of the female to the young*

In most circumstances the female tolerates the presence of the juvenile members in the family group (Fitzgerald, 1935; Epple, 1967*b*, 1970*a*; personal observation, 1971). The female has been observed, nonetheless, to chase young adult females from the family group (Epple, 1967*b*) and to become less tolerant of the young females as they mature (personal observation, 1971). A juvenile *L. rosalia* female was still tolerated at six months of age by both the male and female parents. At nine months she was tolerated less by the female parent upon the birth of twin infants. At 15 months of age the female juvenile assumed a subordinate position to the male and female and to the six-month old male juveniles. She very rarely ate with the family group and food was stolen from her by all of the family members (personal observation, 1971).

The dominant female mother is interested less in the newly born infants than is the male. She involves herself only with the nursing of the infants, and is concerned for a shorter period of time with the infant's whereabouts and well-being than the male (Fitzgerald, 1935; Epple, 1967*b*; personal observation, 1971). After *L. rosalia* young are weaned, they often steal food from the parent's mouth or hands and this food stealing is tolerated (Coimbra-Filho, 1970*b*). Clumsy attempts at allogrooming the parents made by the infants and juveniles are tolerated by the parents in most instances (personal observation, 1971).

(vi) *Relations among the young in the group*

Observers have reported that juvenile members of the group do not establish a dominance hierarchy among themselves, although they display a marked deference toward the dominant group members (Fitzgerald, 1935; Epple, 1967*b*). It was noted that in six-month-old *L. rosalia* juveniles, the larger of the two male twins, in two instances, appeared to be dominant over the smaller. This dominance was noted during both feeding and play periods (personal observation, 1971). As stated above, a 15-month-old juvenile female *L. rosalia* assumed a subordinate position to the six-month-old male juveniles as she became less tolerated within the family unit.

In one *Callithrix jacchus* family unit a pair of young adult female twins was observed to share the responsibility in caring for the new-born infants; i.e. each animal assumed responsibility in carrying one of the newly born twin infants (Lucas *et al.*, 1937). Similar sharing in the responsibility of caring for the infants by group members other than the mother and father has been reported by Epple (1967*b*, 1970*a*). Five days after infants were born to a *L. rosalia* breeding pair, the nine month old juvenile female in the family unit carried one of the infants. It appeared that the infant crawled from the female accidentally. The adult female chased the juvenile until she retrieved her infant (personal observation, 1971). The same juvenile female reportedly began sharing in the responsibility of caring for the infants approximately 16 days after parturition (the juvenile assumed duties in carrying the infants at that time) (DuMond, personal communication, 1972).

(vii) *Intergroup relationships*

Aggressive displays directed toward unknown conspecifics is stronger than those directed at group members. Groups of *L. rosalia*, *Callithrix jacchus*, *M. argentatus argentatus*, *Saguinus*

oedipus (Epple, 1970a) and *S. geoffroyi* (Moynihan, 1970) could not be housed in adjacent cages if visual and olfactory contact could be established without severe fighting resulting. Specifically, the aggression between groups is between the adult males of the two groups and the adult females of the two groups (Epple, 1967b, 1970a, b). When conspecific groups have aggressive encounters, the female has been observed to abort her pregnancy more frequently than under more normal circumstances (Epple, 1970a). If a strange conspecific enters the established home range territory of the family unit, he may be tolerated and ignored (Fitzgerald, 1935), but usually is attacked, fought with and chased from the area by the dominant family members (Epple, 1967b, 1970b). Observations of three family units of *L. rosalia* indicate that although the family units were separated from each other physically, a dominance relationship between the groups appears to exist (personal observation, 1971). The most dominant pair appeared to be a successful feral born breeding pair with one juvenile female offspring and a pair of younger twin male offspring. This pair showed a more complete repertoire of social and sexual behaviors and vocalizations as compared to the other two less successful breeding pairs. They were also older than the other two pairs of animals. The next most dominant pair was a captive born male, whose parents were the above-mentioned most dominant family unit, and feral born female mate. These animals performed a less complete repertoire of social and sexual behaviors and vocalizations. Their behavior patterns were interrupted more frequently by the presence of human beings than were those of the more dominant pair. The least dominant pair was a feral born male and the captive born female offspring of the dominant pair. They had not successfully bred as have the above-mentioned pairs and behaved less like the above two pairs sexually and socially and therefore are considered the most subordinate pair. The female was also quite tame and interacted with human beings frequently.

In the feral environment the territory for each family unit is large and very little overlapping occurs (Coimbra-Filho, 1969; Moynihan, 1970). Coimbra-Filho (1970b) has observed that the placing of *L. rosalia* newcomers in a cage of already established Golden-lion marmosets results in the killing of the newcomer by the dominant members of the established family unit.

(viii) *Relations of one species to another species*

From personal observations (1971) it is noted that aggressive interactions occur between *L. rosalia*, *C. geoffroyi* and *Callimico goeldii*, even though the animals are separated by wire fencing. These interactions occur more frequently during feeding periods, especially when crickets and meal worms are fed, and after the birth of twins to two family units.

Aggressive interactions were seen to occur between *Macaca fascicularis* and the above-mentioned encaged marmosets. In a simulated rain forest environment, *Saguinus fuscicollis* very rarely interacted aggressively with other species of Primates during feedings (personal observation, 1971). Moynihan (1970) reports that in a feral environment *Saguinus geoffroyi*, the Rufous-naped marmoset, has many complex and specialized relations and interactions with other species, especially ecological, geographical and temporal relationships. Direct aggressive confrontations occur rarely. The most obvious interspecies interaction results when the Rufous-naped marmoset comes in contact with birds of prey. The marmoset then usually performs violent escape movements. Often a hawk or buzzard would fly over the cages of three pairs of *L. rosalia*, the initial result being

moving down from higher elevations in the trees, crouching and emitting no vocalizations (personal observation, 1971).

Often rats, mice, and small birds would wander into the cages of three pairs of *L. rosalia*. No aggressive interactions were observed to occur between these animals and the marmosets. The presence of a rat snake within the structure resulted in a general alarm throughout the cages, but no physical interactions. The snake in this instance was in a cage holding *C. geoffroyi*, who appeared curious about the snake and approached it. The cages on either side of the cage with the snake each held a pair of *L. rosalia* with their newly born offspring. The major disturbance was exhibited vocally.

3. Spatial Relationships

(i) Territoriality

L. rosalia and *Callimico goeldii* reportedly scent mark an area repeatedly by rubbing their chest on an object. This type of scent marking involves the sternal gland and perhaps the salivary glands (Epplé & Lorenz, 1967; personal observation, 1971). Epplé & Lorenz have speculated that this activity may represent the marking off of a specific territory. It has been observed that only the dominant males in *Callithrix jacchus* groups demonstrate increased anal scent marking; i.e., the rubbing of the circumgenital area on the surface of an object, as a reaction to any alteration in their environment. This is believed to demonstrate that the dominant male takes the leading role in territorial behaviors (Epplé, 1970b). The male has been observed to recognize the odor of conspecifics from scent marks. These olfactory stimuli tend to elicit aggression from the recipient (Epplé, 1967b). Epplé (1967b) observed anal rub scent marking behavior to occur in all species she studied and to increase after any territorial changes. She observed this behavior in *C. jacchus*, *M. a. argentatus*, *L. rosalia*, *C. leucocephala*, *O. spixi*, *O. oedipus* and *Callimico goeldii*. Apparently, scent marking has a functional significance in the formation of the home range territories established by most marmoset species, although it appears to be more often used as an olfactory display of dominance and as a sexual signal (Epplé, 1967b, 1970a, b).

In a study of feral Rufous-naped marmosets in Panama, Moynihan (1970) reports that *Saguinus geoffroyi* family units each have their own home range, which is defended mainly by hostile display behavior. This hostile display includes attack movements, pilo-erection, attack vocalizations and fighting. The ranges for these marmosets are diverse in shape and large, sometimes extending for more than a quarter of a mile. Moynihan also found that there is very little overlapping of territories by *geoffroyi* units. He also notes that these marmosets move through most of their territory in a day.

DuMond (personal communication, 1971) reports that territorial ranges in a simulated rain forest environment were quite extensive, being four or more acres per social unit in *L. rosalia*, *Saguinus fuscicollis*, *S. oedipus*, and *C. geoffroyi*. He also notes that these marmosets forage in trees at heights no greater than twenty feet above the ground. DuMond hypothesizes that the existence of the limitation in vertical dimension predicates a larger horizontal dimension.

Coimbra-Filho (1970b) observes *L. rosalia* in the feral state to exist in small and scattered groups most frequently located in small trees and swampy meadows. He notes that they rarely move more than a few kilometers from the place where they live and spend the night.

(ii) *Dominance*

The formation of a dominance hierarchy has been observed in most marmoset family units (Fitzgerald, 1935; Epplé, 1967*b*, 1970*a*; DuMond, 1971; personal observation, 1971). The hierarchical unit appears to be a relatively stable formation. In most instances the original alpha male and alpha female remain dominant until their death, if not separated (Fitzgerald, 1935; Epplé, 1967*b*) and if separated the animals usually repair and breed.

The most demonstrable exposition of dominance in the group is displayed by the alpha male and female when the family unit's territory is threatened by a conspecific or by another species. The dominant male and female tend to be more aggressive and display more overt defensive and offensive behaviors in the direction of the territorial intruder while the subordinate members of the family unit display few aggressive behaviors (Epplé, 1967*b*, 1970*a,b*; personal observation, 1971). Epplé (1967*b*) has observed the inferior group members to display certain threat postures and behaviors, but she has not observed them to attack or to fight the intruding conspecific. A juvenile *L. rosalia* female was observed to have aggressive interactions with *Macaca fascicularis* and *Callithrix geoffroyi* (personal observation, 1971). These interactions, although infrequent, consisted of pilo-erection, disturbed vocalizations and actual attack of the other species, which either was walking on the roof of the cage or was in the adjacent cage.

4. Communication

(i) *Tactile signals*

It has been reported that mutual grooming occurs between marmosets, but for the most part the marmoset autogrooms (Moynihan, 1969). From personal observations of *L. rosalia* it was noted that self-grooming involves the use of the hind foot for scratching the skin and combing the fur. The front feet are used for parting fur on the stomach during self-grooming and in allogrooming; i.e. mutual grooming.

Fitzgerald (1935) notes mutual grooming in a colony of *Callithrix jacchus* to consist of the separation of hairs with the fingers and nails and the removal of alien objects by the lips. The groomee approaches the groomer and faces him, lies down in an inviting position, presents back or stomach areas and the groomer approaches and grooms the individual. She also mentions that grooming is extended to the mouth of the groomee, where the teeth are gone over. This type of ritualization and grooming has been observed to occur in *L. rosalia* (personal observation, 1971).

Moynihan (1969) reports that mutual grooming among adults and juveniles occurs in *Callimico goeldii*, *Callithrix jacchus* and *Saguinus geoffroyi*. He notes that extreme alarm seems to inhibit mutual grooming in all species and particularly in the highly excitable *Cebuella pygmaea*. Moynihan (1970) reports that in *S. geoffroyi*, the mutual grooming between mates during breeding season does not usually occur just after copulation. He further notes that if grooming occurs just before copulation, it is distinctively performed with the male as the groomer. Moynihan speculates that because these animals sleep in restricted quarters, the close physical contact provides most of the same social advantages that species often obtain from general social grooming.

From personal observations it may be noted that *L. rosalia* adult males and females frequently groom not only each other, but also their young infants and juveniles. An

increase in the frequency of mutual grooming with the male or the juvenile as the groomer occurred immediately before and after the female gave birth in two separate instances.

(ii) *Olfactory signals*

In captivity *Callithrix jacchus*, *C. leucocephala*, *M.a. argentatus*, *L. rosalia*, *Oedipomidas spixi*, *O. oedipus* and *Callimico goeldii* display scent marking activity (Epple, 1967*b*). Epple notes that frequently the marmoset will sniff the muzzle and genitalia of group mates, sexual partners and unknown conspecifics. She notes that the dominant male and female tend to display more scent marking behavior than the subordinate group members. An increase in scent marking occurs after sexual encounters, alterations in territory (Epple, 1967*b*; personal observation, 1971), aggressive interspecies interactions (personal observation, 1971) and hostile episodes with group members of the same sex or after the introduction of a strange conspecific into the organized group (Epple, 1967*b*, 1970*a, b*). Marking apparently functions as a sexual signal, territorial signal, and as an olfactory display of dominance. Scent marking activity was observed to occur after arched back and pilo-erection display of one male mate in a successful breeding pair of *L. rosalia*. This arched back and pilo-erection appeared to be in some instances either nondirective or directed at the observer (personal observation, 1971).

Sternal gland marking behavior was studied in *C. jacchus*, *M.a. argentatus*, *L. rosalia*, *Tamarinus imperator*, *O. oedipus*, *O. spixi*, and *Callimico goeldii* (Epple & Lorenz, 1967). Moynihan (1970) studied this behavior in *S. geoffroyi*. Epple & Lorenz note that the movements and postures during the marking procedure are similar in Callithricidae, varying only to the object being marked. The general procedure is for the chin and chest to be rubbed several times against the object in a downward direction, while the rump is either pulled by the arms or pushed by the legs and the other pair of limbs hang freely. *L. rosalia* and *Callimico goeldii* frequently scent mark the same area and Epple & Lorenz speculate that this is a form of territory marking. They also speculate that sternal gland marking is a form of social sexual communication, but that it occurs less frequently in this capacity than marking with secretions from the circumgenital skin glands.

Anal rubbing scent marking in *C. jacchus* is performed frequently during daily routine (Epple, 1967*b*). Epple notes that the circumgenital area is rubbed against objects in the environment and only rarely against the body of a group mate. The fluid used in anal scent marking is a composition of secretions from the apocrine and sebaceous glands, which cover the genitals and the circumgenital area, plus a few drops of urine. Marmosets displaying this type of scent marking are *C. jacchus*, *C. leucocephala*, *M.a. argentatus*, *L. rosalia*, *O. spixi*, *O. oedipus* and *Callimico goeldii* (Epple, 1967*b*).

DuMond (personal communication, 1971) noted that when *L. rosalia*, *C. geoffroyi* and *C. goeldii* were placed in new, large cages they began scent marking their new territory and that after a period of time the frequency of scent marking decreased significantly. Epple (1970*b*) speculates that scent marking as an olfactory signal apparently is important in sexual communication, territoriality and display of dominance.

Moynihan observed sternal scent marking and circumgenital scent marking in *Saguinus geoffroyi*. He observed that in the wild most scent marking is done against branches, while in captivity the marmoset may rub against many different surfaces and objects. *L. rosalia* mark most frequently by sternal marking, but also circumgenital scent mark wire fencing, wooden doors, metal sheeting, cement and pain coated floors and walls as

well as tree branches (personal observation, 1971). Moynihan believes that circumgenital marking occurs during less hostile encounters than sternal marking. He hypothesizes that scent marking is an aggressive, hostile display, usually performed by an animal protecting his territory from an intrusion by another animal.

Sternal scent marking is displayed more frequently in *L. rosalia* by the adult male in the family unit than is circumgenital scent marking. Sternal scent marking can be conspicuously observed throughout the year. The possibility exists that circumgenital scent marking may be important in social-sexual communication between groups and within the family unit in *L. rosalia* (personal observation, 1971). Scent marking, both sternal and circumgenital, occurred less frequently in the purportedly dominant successful breeding pair than in either of the other two cages observed.

Circumgenital scent marking may be an important factor in explaining the difficulties in breeding captive born *L. rosalia* successfully. In some species of animals, such as mice (Bronson, 1971) and Mongolian gerbils (Thiessen, 1968; Thiessen, *et al.*, 1968; Thiessen & Yahr, 1970), scent marking is important in sexual communication and may cause delay in puberty, synchronization of estrus, pregnancy block and anestrus. Scent marking substances may initiate and maintain pair bond formation by acting as a sexual attractant. Puberty may be delayed in *L. rosalia* juveniles in that no sexual behavior was observed between the adult parent and the juvenile animals (personal observation, 1971). The possibility exists that the male inhibits the onset of puberty in male juveniles and so the juvenile males appear sexually unattractive to the adult female. The female inhibits the onset of puberty in the juvenile female perhaps through the production of specific chemical scents and thus prevents the female from appearing sexually attractive to the male parent.

The possibility of the synchronization of estrus in the female by the male may result through the emission of chemical substances via circumgenital scent marking, which are received by the female and are physiologically translated through neuroendocrinological networks to set off ovulation. Because no external sign exists when the female is in estrus and because the female *L. rosalia* can become pregnant and give birth in any month of the year, it can be hypothetically speculated that a synchronization of estrus occurs (personal observation, 1971). The following behavior patterns may occur as correlates to the ongoing physiological processes: the male and female emit chemical substances through the sternal gland, which act as sexual attractants and aid in the formation of pair-bonding and in the recognition of individuals. Substances may be emitted through the circumgenital glands and may function as sexual attractants also. The circumgenital scent substances which the male emits are differentiated by the female by means of neuroendocrinological networks. Ovulation is set off after stimulation by the male chemical emissions. The female then emits chemical substances which attract the male and tell the male that the female is in estrus. It is at this time that sexual behavior is observed and the male stays in close proximity of the female.

(iii) *Visual signals*

It has been reported that marmosets have no power of grimace and have little power of complex facial expression, i.e. facial expressions play an insignificant role in social communication in marmosets (Hill, 1957; Moynihan, 1969). When *L. rosalia* juveniles or adults are startled by either a human being or another animal, they display their

teeth, raise their eyebrows, squint, pull the corners of their mouths back, and jerk back their heads (personal observation, 1971).

Epple (1967*b*) has reported the following visual signals to occur during aggressive threat displays in *C. jacchus*, *C. leucocephala*, *M.a. argentatus*, *L. rosalia*, *O. spixi*, *O. oedipus*, and *Callimico goeldii*: (1) Lowering of the eyebrows occurs in *C. jacchus*, *C. leucocephala*, *M.a. argentatus* and *C. goeldii*; extreme lowering of the eyebrows and significant protrusion of the lips occurs in *O. spixi* and *O. oedipus*. (2) Pulling back the corners of the mouth and flattening of the ears and/or ear tufts occurs in all species. (3) Lip-smacking and rhythmic protrusion of the tongue occurs during sexual, social and aggressive threat contacts. (4) Pilo-erection is part of the aggressive threat complex in *C. jacchus*, *C. leucocephala* and *M.a. argentatus*. (5) Arching the back, a posture assumed in defensive threat, occurs in all the species studied except *Oedipomidas*. (6) Presentation of the genitalia by *C. jacchus*, *C. leucocephala* and *M.a. argentatus* is not an invitation for mounting nor a submissive behavior, but rather it is an aggressive threat visual signal usually assumed by the dominant members of the family unit.

(iv) Acoustic signals

Fitzgerald (1935) reports that in captive *C. jacchus* a disturbed state is spread to other group members through voice contact. Vocalization and movement are important infant stimuli necessary for parental behavior responses to occur. If the newly-born infant does not emit vocalizations and non-directed movement immediately following birth, then the parents will ignore that individual completely (Epple, 1970*a*).

Epple (1967*b*) believes that vocalization and crouching by an inferior animal while sniffing a presenting dominant animal is also an important set of signals in the socio-sexual behavior complex. When marmosets are confined in small enclosures, they sometimes are inactive and display a limited repertoire of social responses and vocalizations (Epple, 1970*a*).

The vocal repertoire of adult marmosets is relatively stereotyped and highly stereotyped in *L. rosalia*, *C. jacchus*, *C. leucocephala* and *M.a. argentatus* (Epple, 1968). Epple (1967*b*) believes that since marmosets display few facial expressions and postures serving as social signals, the function of vocalizations becomes paramount in importance.

Andrew (1963) believes the main type of vocalization in marmosets to be the twitter. Epple (1968) believes that the basic element of all vocal signals to be the "phee" call, a short, monosyllabic call. Epple's reasoning is that in the infant marmoset the "phee" call seems to be the vocalization from which other adult notes develop. Observations of infant, juvenile and adult *L. rosalia* vocalizations support Epple's reasoning (personal observation, 1971).

5. Sexual Behavior

Socio-sexual signals. No external signal that the female marmoset is in estrus has been observed (Lucas *et al.*, 1937; Hill, 1957; Epple, 1967*b*; personal observation, 1971). Russell & Zuckerman (1935) have reported an observed swelling in the circumgenital area of a dead female marmoset, that was not identified specifically, but was thought to be either *C. jacchus* or *C. albicollis*. No other reports to date have verified this findings. Epple (1967*b*) reports slight swelling of the circumgenital region in *C. jacchus* female.

during increased sexual activity, but she believes that the swelling is insignificant in the sexual relationship.

The female marmoset is not sexually attractive to the male at all times (Lucas *et al.*, 1937; personal observation, 1971). Apparently the best indication that the female is in estrus is courtship and mating (Epple, 1967*b*). Fitzgerald (1935) reports that in *C. jacchus* the sexual partners do not examine each others genitalia nor do they show public display of sexual emotions. During copulation the animals engage in long and intense staring, open and close their mouths with frequent moistening of the lips and emit no sounds. Epple (1967*b*) observes sexual play to occur in *C. jacchus* partners. Behaviors include walking in the arched back posture, scent marking, sniffing partner's scent marking sites and genitalia, lip smacking by the male, protruding of the tongue rhythmically and licking and combing the partner's fur with the incisors. In *O. spixi* no walking in the arched back posture or licking and combing of the partner's fur with the incisors occurs. In this species the female curls her tail under her body and saturates it with urine and secretions from the circumgenital area. The male then proceeds to sniff the tail (Epple, 1967*b*).

Sexual behavior occurs after parturition in *L. rosalia* (personal observation, 1971). The only noticeable behavior pattern is that the male stays in close proximity of the female at all times and spends much of his time grooming the female or resting next to her and sniffing areas where the female sat. Copulatory behavior occurred in two breeding pairs of *L. rosalia*, both being very quick episodes, both following parturition, and both being unsuccessful fertilizations.

C. jacchus sexual activity is high following parturition (Epple, 1967*b*). Epple reports that after approximately three days following parturition, the male becomes sexually interested in the female, but that usually the female rejects him and only gradually becomes more attentive to the male advances. The first copulation occurs 7–10 days after parturition with sexual activity increasing until day 10, after which time it gradually decreases. After this time copulatory behavior occurs infrequently, but occasionally occurs even during pregnancy. The female can become pregnant twice a year, which may indicate that in captive *C. jacchus*, there occurs at least one post-partum estrus between each two pregnancies (Epple, 1967*b*). No one has determined definitely the factors involved in the regulation of the breeding cycle in captive or feral marmosets.

The following is an example of two *L. rosalia* birth episodes and the behaviors which followed parturition (personal observation, 1971).

1–4 days after parturition	copulatory behavior observed
male begins to pay more attention to the female (sniffs genitalia and scent marks)	the second and third day after the second birth episode, which followed one week after the first birth episode (the sexual behavior occurred in the later birth episode parents and in an unsuccessful breeding pair)
male stays in close proximity of the female adult mother	
transfer of infants to the male for carrying (on the third day in one instance and on the seventh day after parturition in the other instance)	

The possibility that copulatory behavior in *L. rosalia* occurs in the animal's sleeping quarters also exists (DuMond, personal communication, 1971), in that in this Primate species the male and female sleep together at night. *L. rosalia* behavior patterns are interrupted easily by any sudden movements by human beings, noises, and interspecific interactions. Moynihan (1970) reports observing no copulations in the feral environment of *Saguinus geoffroyi* and he believes that the presence of human observers may be a disturbing element. It is therefore also possible that copulatory behavior is not observed frequently in captive marmosets due to interruptions in their external environment.

Epplé (1967b) speculates that menstrual bleeding is inconspicuous in the female marmoset, and that it may be seen only in vaginal smears. Olfactory signals play a significant role during the period of estrus. It is possible that scent marking and sniffing of the genitalia may be specialized behaviors developed to compensate for the non-appearance of cyclical circumgenital swelling. Scent marking regularly precedes and follows copulation in *C. jacchus* (Epplé, 1967b). Epplé observes scent marking and the sniffing and licking of the partner's genitalia to be a regular component in courtship behavior in marmosets. She notes that the submissive and juvenile group members display infrequent scent marking behavior, which increases only during copulatory behavior of the breeding pair.

DuMond (personal communication, 1971) notes that *S. fuscicollis* living in a simulated rain forest environment has given birth to seven sets of twins. It appears that the same female is the mother on all seven occasions, although various male members of the troop have carried the young.

From personal observations (1971) of *L. rosalia* and a report by Moynihan (1970) on *S. geoffroyi*, copulatory technique is noted as the following. The male mounts the female from the rear, sitting behind and partly on top of her. He clasps her tightly around the waist with his arms and grasps the perch with his feet. It appears that the penis is inserted almost immediately and pelvic thrusts begin. The number of insertions varies, and with less insertions it becomes more difficult to observe the behavior. After a successful copulation the male may be seen to lick his genitalia.

6. Breeding Problems in *L. rosalia*

In the captive environment, mismanagement and health and nutrition problems have led to a decrease in population density of *L. rosalia*. Parasites, trauma from shipping, improper and insufficient diets and climatic conditions have added to the decimation of this New World monkey. Correction of these problems does not eliminate the causes for decrease in population density in captive circumstances. The Golden-lion marmoset has an expected life span of approximately 10 years. The last feral born *L. rosalia* received in the United States were delivered between 1966 and 1968. The youngest U.S. feral born animals are now five and six years old. Feral born *L. rosalia* mates usually are successful breeders. Instances of breeding pairs consisting of a feral and captive born animal do occur. In 1971, a captive born male and a feral born female at Monkey Jungle in Goulds, Florida, successfully bred and reared twin male Golden-lion marmosets (personal observation, 1971). Coimbra-Filho (1972) reports the success of a feral born male and a captive born female combination and a feral born female and a captive born male in breeding. No successful breeding has occurred between two captive born paired *L. rosalia*. It is important to note that heterozygous twinning is usual in the birth

episode. The twins are chimeric for blood, splenic tissue, lymph node, bone marrow and testicular tissue (Hampton & Hampton, 1965). Hampton & Hampton (1965) report that the placenta has an enzymatic function which appears to prevent free-martinism.

The solution to the difficulty encountered in breeding *L. rosalia* in captivity remains unfound. The study of the social and sexual behaviors of the Golden-lion marmoset is an important step in better understanding problems complicated by an artificial environment. Important questions, as yet unanswered, concerning the problem of successful breeding of *L. rosalia* include the following: (1) What is the length of the estrus cycle, its onset and its offset? (2) Does a post-partum estrus exist for certain, what is its specific function? (3) What are the specific behavioral correlates before, during and after estrus? (4) Is the adult male necessary in rearing the young? (5) When is it best to separate breeding pairs? (6) What are the dynamics of pair-bond formation? (7) At what age should juveniles be removed from the family unit to prevent the delay of maturation? (8) How can pregnancy be detected in its early stages?

A meeting on *Leontopithecus rosalia* in February 1972, sponsored by the Wild Animal Propagation Trust has determined the minimum requirements for the maintenance of *L. rosalia* in captivity. WAPT has designated various zoos throughout the United States as special breeding centers for this marmoset species. The minimum requirements for maintenance include cage design, diet, medical problems, animal transportation, animal keeper regulations and data collection and research methods.

DuMond (1971) has suggested that a critical period in juvenile *L. rosalia* behavioral development is missed by captive-born animals. This period includes separation from the parental unit and pair-bond formation. The specific time and the way in which juvenile Golden-lion marmosets leave the parental unit to form pair-bonds in the feral environment is not known. Information concerning the formation of a new territory in the feral environment is not available.

Reproductive failure of *L. rosalia* captive-born mates is not probably the result of one specific factor, but rather the combination of many. A chemical-sensory regulatory theory, such as a pheromone theory, to explain delay in puberty, pair-bond formation, sexual attraction, and synchronization of estrus has yet to be proven. Presently, behavioral evidence exists for correlation between complex chemical interactions and reproductive functioning; however, substantial physiological evidence does not exist. The complete answer to successful breeding of captive-born mates remains a mystery. A solution to breeding problems in the captive environment between captive-born mates must be found quickly. At the present rate, the extinction of *Leontopithecus rosalia* will occur between the next five to ten years.

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R. Fenart

Sexual Differences in Adult Skulls of *Pan troglodytes*

R. Deblock

Laboratoire de Craniologie comparée
E.R. 93 du C.N.R.S.,
Faculté Libre de Médecine,
56, rue du Port, Lille Cedex 59046,
France

The sexual differences of the skull of *Pan troglodytes* have been established on 342 classic and vestibular measures taken on 19 male and 23 female skulls. The Students' *t* test has revealed 98 significant parameters with a reliability of 99%. They indicate a greater importance of the naso-frontal zone and of the facial mass in the male. On the other hand the most significant widths are situated in the retro-vestibular zone.

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1. Introduction

Following recent research work (Fenart & Deblock, 1972) on sexual differences in the skull of Man and the dwarf chimpanzee (*Pan paniscus*), such differences have now been studied by us in *Pan troglodytes*, the common chimpanzee. The present work must not be considered complete in itself, but as part of a comprehensive inquiry aimed at studying the skull from different types of chimpanzee, with different techniques.

Our investigations have been carried out by resorting to the Students' *t* test. Although analysis of discrete parameters by this method does not show the possible correlations existing between some of them, a problem now being studied with a computer, we thought it of use for the preliminary clarification of some characteristic features. Accordingly, the *t* test has been applied to 342 measurements (linear, angular, ponderal and volumetrical, relations and index) taken on 19 male and 23 female skulls from *Pan troglodytes* made available to us, for the most part, by the Royal Museum of Central Africa in Tervuren (Belgium).

In our measurements, data of classical craniology are supplemented with the parameters obtained by orientation of the skull according to the vestibular axes, such as the vestibular coordinates (*x* and *y*) of the main craniometrical points.

From this research it emerges that 98 parameters (above 30%) have proved significant with a reliability of 99% and 37 (40%) with a reliability of 95%.

The list of parameters significant at 99% and the averages for adult males ($V\sigma$) and females ($V\varphi$) are reported in Table 1. The abbreviations used both in the table and the drawings are as follows:

Aa	Upper oblique width of the ascending branch of the mandible.
a'	Anterior part of the superior alveolar edge between the prosthion and the foot of the perpendicular drawn from the anterior sifted on this edge.
AB	Whole mandibular length on the inferior alveolar edge.
A'B'	Whole projection of the mandible on the mandibular plane.
Ac.i-C.a.	Distance: internal acrion-anterior sifted.
Al.i.	Inferior alveolar point.
a.n.	Angle: nasion-centre of the axes-horizontal vestibular plane (anterior part).

Ant	The most anterior point of neurocranium (in vestibular orientation).
A ₁ Z	Maximal height of neurocranium above Frankfurt plane.
b'	Posterior part of the superior alveolar edge between the foot of the perpendicular drawn from the anterior sifted on this edge and the ptérygo-alveolar point.
Ba	Basion.
Ba-Br	Distance; basion-bregma.
Ba-C.a.	Distance; basion-anterior sifted.
Ba-Pr	Distance; basion-prosthion.
b.cr.	Expanded bi-crest width.
BE	Distance; condylian point-inferior alveolar point.
b.inc.	Bi-incisural width.
BL'	Maximal symphysary length.
bl	Maximal symphysary width.
b.m.e.p.	External bi-molar width measured on the superior maxillary (between M ₁ and M ₂).
b.m.i.	Bi-maxillo-incisive width, at the junction of the external alveolar edge and the maxillo-premaxillary suture.
b.m.i.p.	Internal bi-molar width measured at the same place as b.m.e.p.
b.m.m.	Maximal bi-mastoidian width.
b.po.	Distance between the two porions measured on the inferior part of the cranium.
b.Po.d.	Expanded bi-porion width.
Br	Bregma.
b.z.a.	Anterior bi-zygomatic width.
b.z.m.	Maximal bi-zygomatic width.
b.ε	Inter-temporo-parietal width, between the points ε, replacing of euryon and situated at the junction of temporo-parietal suture and fronto-vertical vestibular plane.
β	Angle of the alveolar plane with the direction of the posterior edge of the ascending branch of the mandible.
β'	Angle of the base of the mandible with the direction of the posterior edge of the ascending branch of the mandible.
C.a.	Anterior sifted.
c.a.e.-Br.	Auricular radius of bregma.
c.a.e.-I	Auricular radius of inion.
c.a.e.-Pr.	Auricular radius of prosthion.
c.b.v.	Angle; posterior sifted-basion-horizontal vestibular plane; this angle is positive when the basion is at a lower level than the posterior sifted.
CD'	Coronoidian height above the mandibular plane.
Cor	Coronoidian point.
C.p.	Posterior sifted.
d _{po}	Distance between the porion and the surface of the bi-parietal sphere.
d _{po} /R	Index of relative distance between the porion and the surface of the bi-parietal sphere.
d _{py}	Distance between the pterygo-alveolar point and the surface of the bi-parietal sphere.
EF	Condylian height on the alveolar plane.
EF'	Condylian height on the mandibular plane.
Eg	Distance; gonion-condylian point.
EL'	Distance; condyle-symphysal lower point.
fl.4	Length of the arrow of the arch; Ac.i.-Op
f.m.e.	External bi-fronto-malar width.

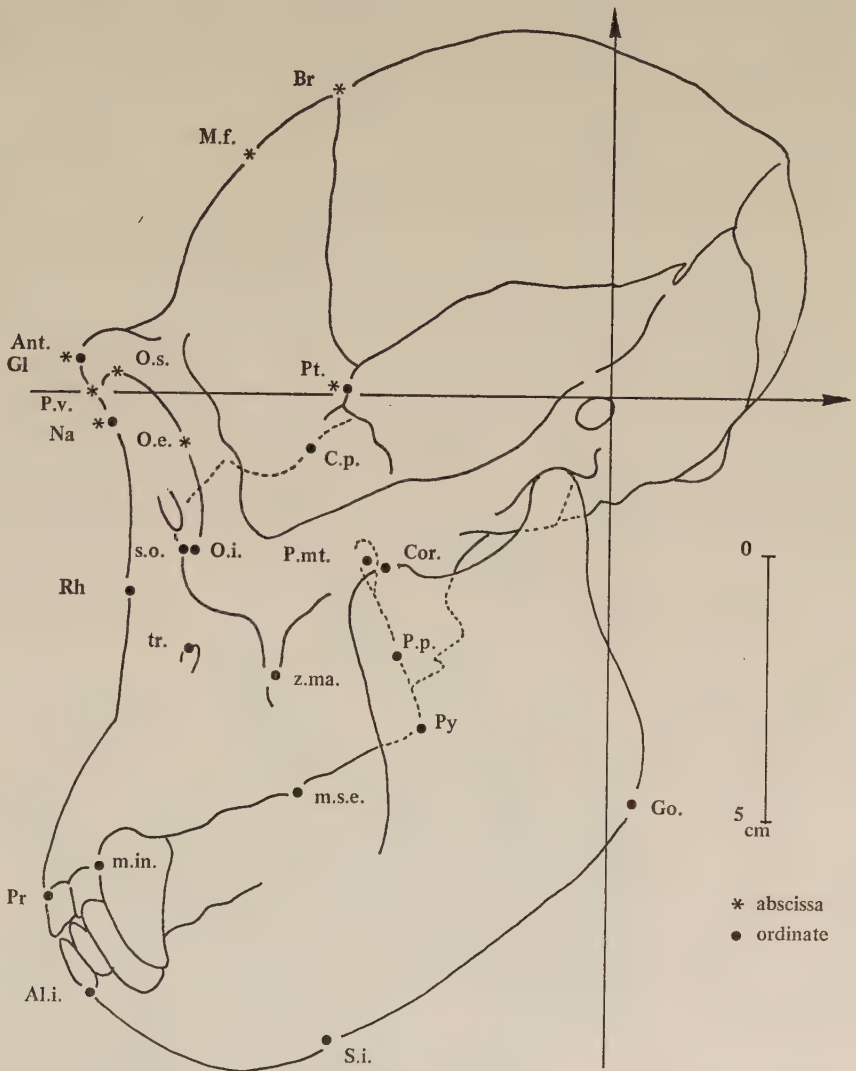
f.m.i.	Internal bi-fronto-malar width.
gg'	Bi-goniac width.
Gl	Glabella.
Gl-I	Distance: glabella-inion.
Gl-L	Distance: glabella-lambda.
Go	Gonion.
h	Height of the endo-face: length of the perpendicular drawn from the anterior sifted upon the superior alveolar edge.
Hg	Oblique width of the ascending branch.
I'J'	Distance between the chin hole and the mandibular plane.
I-Pr	Distance: inion-prosthion.
l.b.s.o.	Distance between the maxillo-malar points situated on the orbital rims.
l.c.s.	Mesio-distal width of the crown of the upper canine tooth.
L.pa.	Length of the palate.
M.f.	Medio-frontal point.
m.in.	Maxillo-incisive point.
m.s.e.	External superior molar point.
Na	Nasion.
Na-Ba	Distance: nasion-basion.
Na-Op	Expanded distance: nasion-opisthion.
Na-Pr	Distance: nasion-prosthion.
O.e.	External orbital point.
O.i.	Inferior orbital point.
Op-Na	Distance: opisthion-nasion.
O.s.	Upper orbital point.
P.mt.	Metafacial point.
Po-Br	Distance: porion-bregma.
P.p.	Posterior palatine point.
Pr	Prosthion.
Pr-N	Distance between the prosthion and the Frankfurt plane.
Pt	Pterion.
P.T.	Weight of the mandible.
P.v.	Prevestibion.
P.V.I.	Maximal internal prevestibular length.
P.V.T.	Maximal external prevestibular length.
p.v.t.	Maximal post-vestibular, external length.
Py	Pterygo-alveolar point.
Rh	Rhinion.
R'R''	Maximal bi-condylar width.
r.p.p.	Radius of the peri-parietal circle.
S.i.	Symphysal lower point.
s.o.	Orbital lower point on the maxillo-malar suture.
Σ	Frontalization angle.
t	Basi-occipital, external angle with the vestibular horizontal plane.
t.m.	Width between the chin holes.
tr	Hole under the orbits.
u	Distance between the central point of the axes and the intersection of the vestibular horizontal plane and the direction of the pterygo-maxillary line.
v	Distance between the centre of the axes and the point of intersection of the vestibular horizontal and the orbito-mandibular line.
Vol	Cranial capacity.
z.m.	Bi-zygo-maxillary width, taken at the lower part of the suture.
z.ma.	Zygo-maxillary point.

2. Coordinates

To facilitate the interpretation of the results, let us consider first the vestibular coordinates of the craniometrical points: a significant value of t will indicate, a different position between the ♂ and the ♀, from the point which is considered, either in the horizontal sense (abscisse) or in the vertical sense (ordinate).

It may be noticed, first of all, that there are more points differing in their ordinate than in their abscisse position. Sexual characteristics stand out especially in the vertical sense (the skull being oriented according to the vestibular axes). The points having a different position in the abscisse are preferentially grouped in the fronto-nasal area. From the nasion to the bregma, through the Torus supraorbitalis the profile is much more advanced

Figure 1. Coordinates.



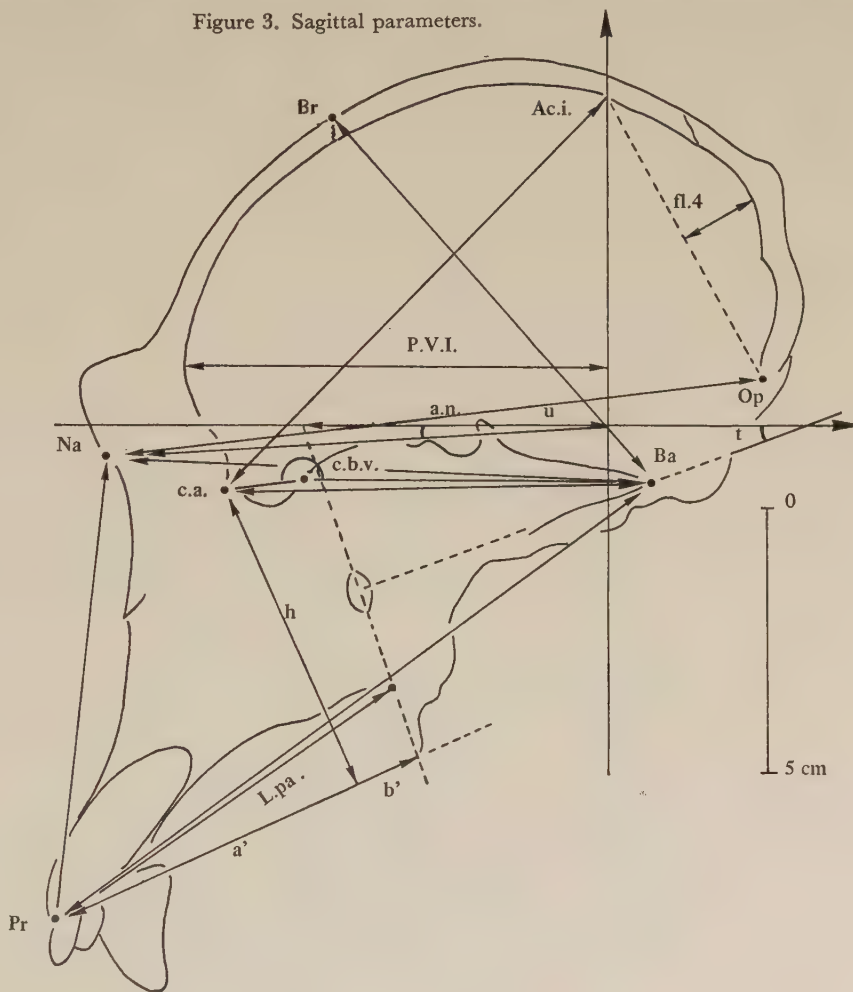
3. Cranio-facial Measurements

The analysis of the "direct" measurements leads to several global findings. (a) The mesio-distal width of the crown of the upper canine tooth (l.c.s.) far exceeds the other parameters with a t higher than 10; so, it is the best "sexual" measure in *Pan troglodytes* (as was the case in *Pan paniscus*). (b) The whole cranio-facial shows more discriminative measures than the mandible alone. (c) The linear measures characterizing sexual differences are more numerous than the angular measures, those of volume and relationships.

It is therefore advisable to consider, first, the linear parameters of the cranio-facial entirety.

Among the measures of *lengths* (this term is used here in a very broad meaning) we find those which confirm the furtherance of the frontal of the ♂ in relation to that of the ♀ as well as for its internal and external tables. A bigger frontal sinus and a more prominent frontal torus are not the only elements concerned. Both these parameters are considered, at the back, from the basion or from the vestibular vertico-frontal plane or even from the opisthion (Figures 2 and 3). In connection with the foregoing description, we notice that

Figure 3. Sagittal parameters.



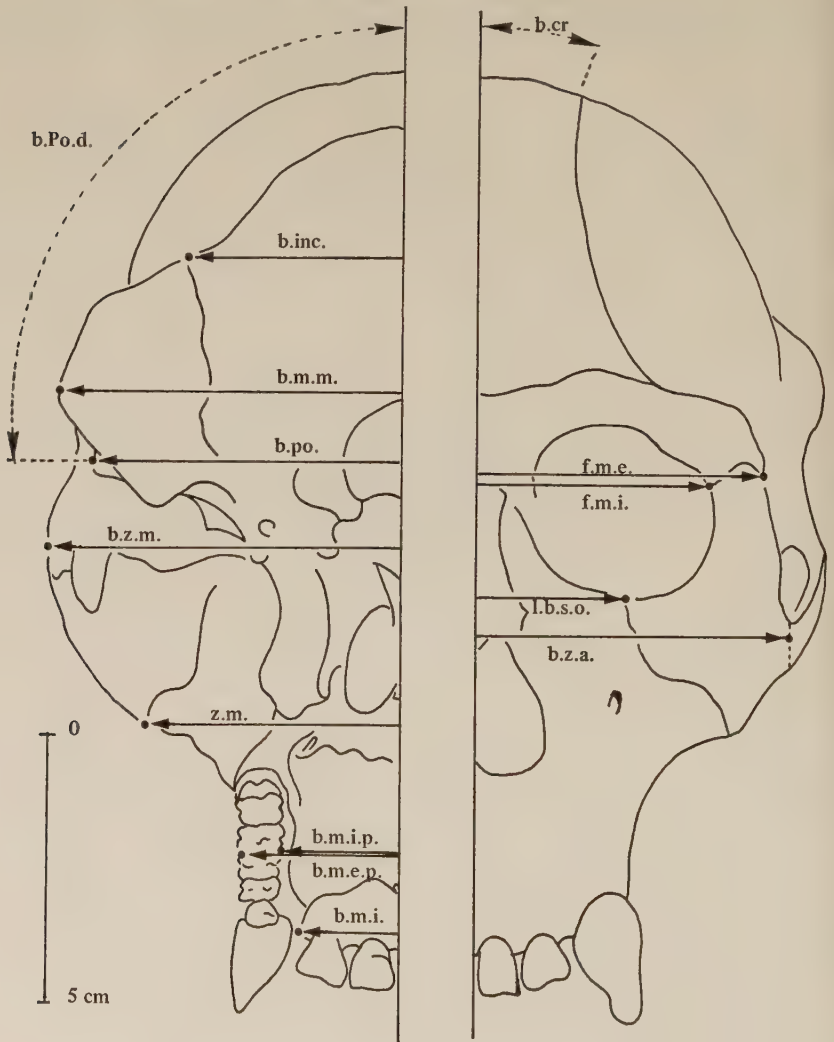
the relation between the ante-vestibular and the retro-vestibular skull is significant at 99%.

If we consider some lengths taken more obliquely (for instance from the inion to the glabella or to the prosthion, or from the glabella to the lambda) the values of t are still very high and, among the ♂, the cranio-facial lengths are significantly higher than among the ♀.

Other measures of lengths concerning more particularly the facial mass (from the basion to the nasion or to the prosthion, from the prosthion to the external auditory duct) show that the latter is more elongated in the male. This is also true for the alveolar edge and the differences remain highly significant.

Among the parameters specifying the notion of *height*, some of them arising in the zone surrounding the external auditory duct and reaching the roof near the bregma show a

Figure 4. Transversal parameters.

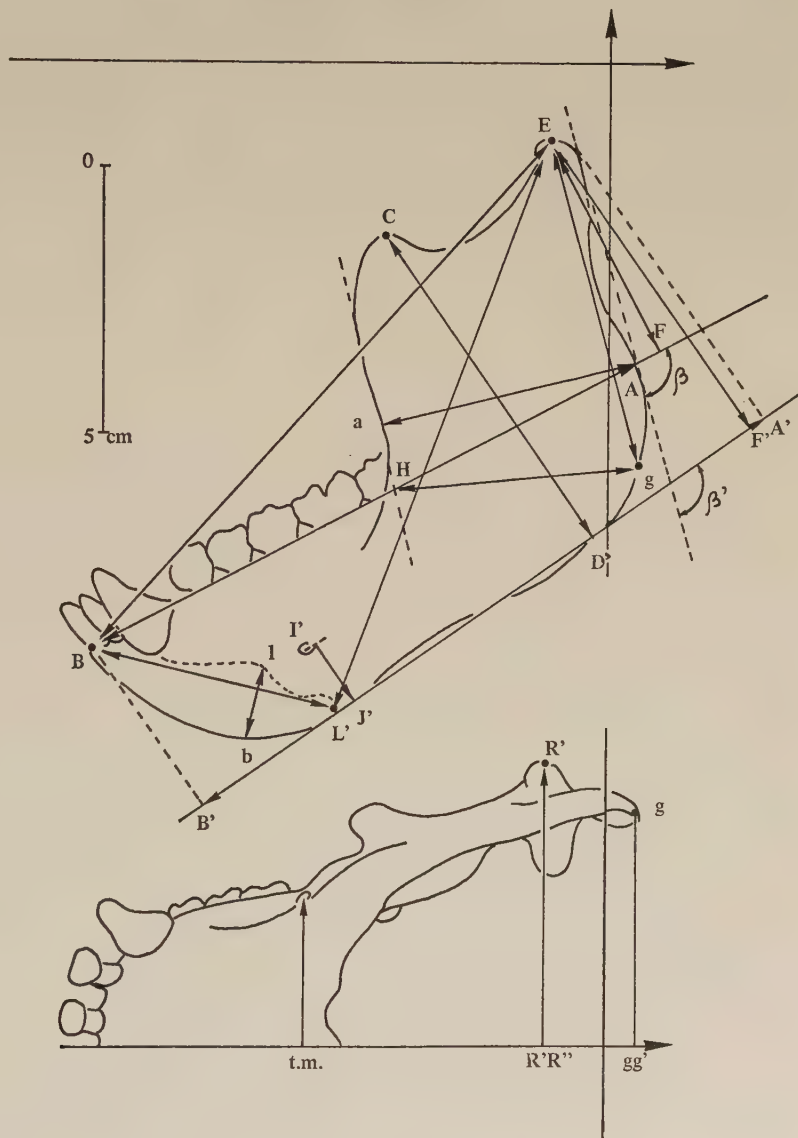


significant t proving that the neurocranium (according to an orientation close to the Frankfurt plane) is higher in the ♂ than in the ♀. This finding is confirmed by a difference of the oblique dimensions such as C.a.-Ac.i. and Ba-Br.As regards the vestibular orientation, the height being measured toward the back is not significantly different.

To these findings, we must add an increase of height of the facial mass either measured from the anterior sited, perpendicularly to the alveolar edge or from the nasion (to the prosthion). The facial height taken under the Frankfurt plane is also significantly greater in the ♂.

Let us now examine the third dimension: the *width* (Figure 4). It is significantly bigger in the ♂ for numerous parameters of the rear-skull (especially at the level of the

Figure 5. Mandibular measures.



porion and of the mastoid) and of the face (at the levels: orbital, anterior zygomatic, zygo-maxillary) and of the palatine roof (both the level of the molars and the maxillo-incisive suture). Between the anterior facial zone and the rear-skull, the only maximal bi-zygomatic is distinctly significant ($t = 5.87$).

Given the increase of the three cranial dimensions in the ♂ in relation with the ♀, it is not surprising to notice that it is the same for the cranial capacity ($t = 3.93$). However, the radius of the bi-parietal sphere does not belong to the parameters having a t higher than 2, this is explained by a discrepancy between shape and volume. As regards the angular values, we point out the angle of orbitary frontalization which is flatter in the ♂ than in the ♀.

4. Mandibular Measurements

Finally, after the cranio-facial mass, we must consider separately the mandible (Figure 5) where one of the highest values of t is that of the weight of this bone ($t = 4.81$).

Apart from two angles which prove that, in relation to the body of the mandible, the posterior edge of the ascending branch is more oblique in the ♀ than in the ♂ the measurements taken on the lower jaw prove, by the t test that the latter are significantly bigger in the ♂ in the 3 directions: lengths (taken according to the inferior alveolar edge or from the condylian point) heights of the ascending branch (as much at the coronoidian point as at the condyle) and posterior and anterior widths.

5. Conclusion

With the skull being oriented according to the vestibular axes and the significance of the statistical results being fixed at 99 % reliability, the sexual differences of the skull of *Pan troglodytes* reflect a higher general value of the dimensions of the head in the male. Precise analysis shows a greater sagittal development in the pre-vestibular as compared to the retro-vestibular zone, whereas differences in width are more marked in the latter.

We must point out that in the male the naso-frontal area is more advanced and the facial mass larger than in the female, with a more extensive metafacial zone. The result is a lowering of the alveolar edges and of the whole mandible, excluding the condylian zone. The angular values are not significant. Finally, this work confirms the importance of the endocranial cubage and the value of the mesiodistal diameter of the crown of the upper canine tooth for the assessment of sexual differences in the Primates.

When we compare the present results with those obtained in *Pan paniscus* (in which 37 sexually significant parameters with 99 % reliability were found) quite considerable differences between the two species come to light. In *Pan paniscus* only the splanchnocranium is more developed in height and then only in its posterior region; the frontal part is not sexually characteristic; the cranium lengths do not discriminate much but for the projection of the external orbitary rim. As regards the measures of width, except the bi-alar diameter (sphenoidal), all the parameters of some interest are found toward the back, both in the mandible and the cranium. *Pan paniscus* presents by far fewer parameters whose levels reach 2.6, than *Pan troglodytes*. Hence it is much easier to find out, with the t test, the sex of a cranium from a common than from a dwarf chimpanzee.

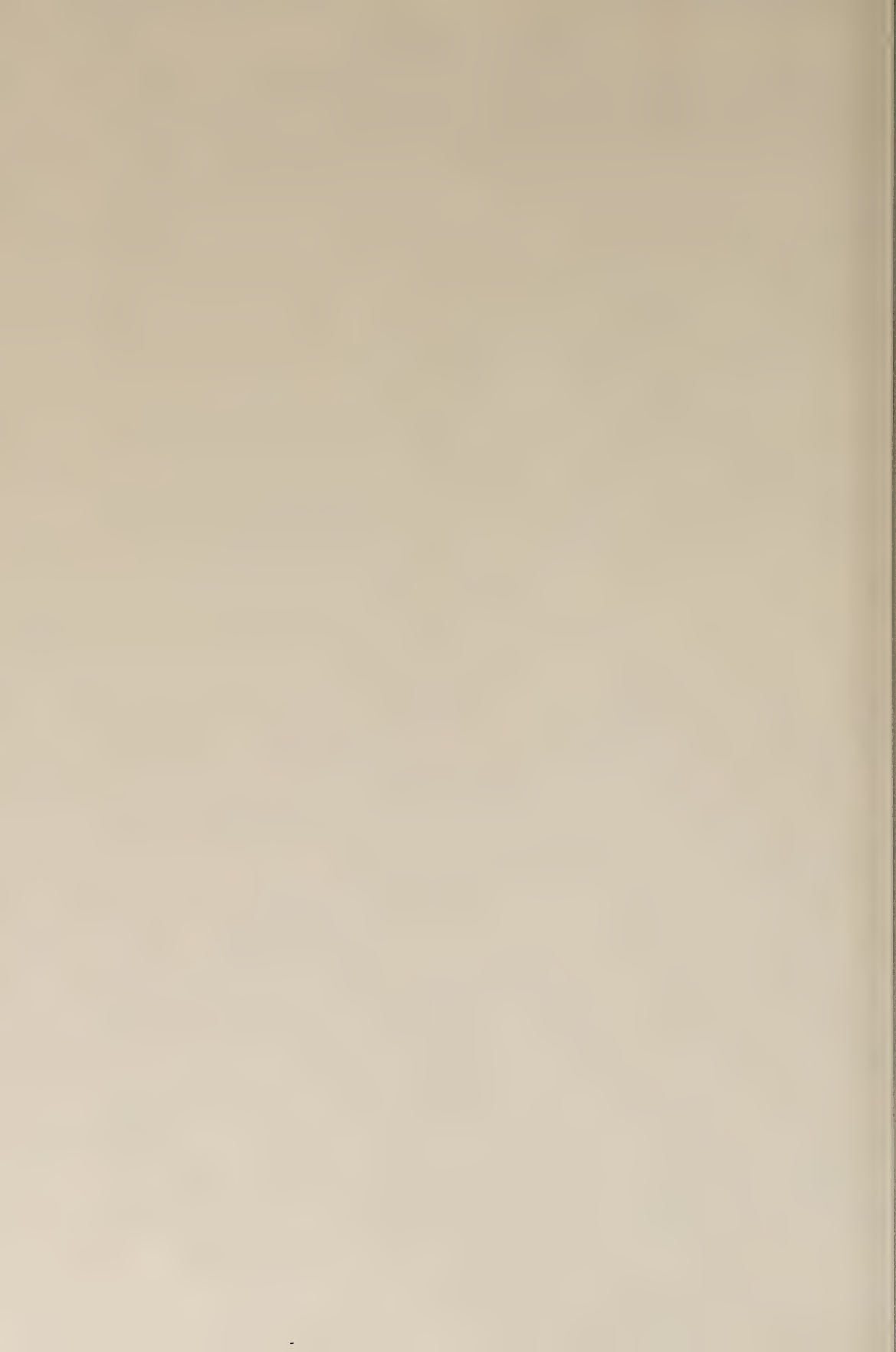
As stated above, other statistical methods have been used in connection with the present problem such as the rate of distance from the equiprobable ellipses, calculation and

drawing of the frontier lines between the scatter diagrams and discriminant multifactorial analysis. They will be dealt with later.

At any rate, the dissimilarity in the sexual points between *Pan troglodytes* and *Pan paniscus* is in favour of the specific duality of these two species of Primates.

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Daris R. Swindler

Frank J. Orlosky

Department of Anthropology and
The Regional Primate Research
Center, University of Washington,
Seattle, Washington 98195,
U.S.A.

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Metric and Morphological Variability in the Dentition of Colobine Monkeys

A morphological study was performed using 97 *Colobus polykomos* and 41 *Nasalis larvatus*. The premolars and molars of these two taxa of leaf-eating monkeys were similar in that they possessed deeply grooved and highly pointed cusps. Of 7 dental traits investigated, 4 were significantly different between the 2 forms. Indeed, with 2 of these, the position of the lingual cusp on PM₄ and the number of cusps on PM₃ displayed highly contrasting structures.

Metric analysis was conducted using 47 *C. polykomos* and 37 *N. larvatus* specimens. Mesiodistal and buccolingual measurements were taken on the upper canine and all postcanine teeth. Sexual dimorphism was detected in most maxillary dental measurements and all mandibular estimates of both species. In all cases, males exceeded females in tooth diameter. Testing between species by sex revealed that *C. polykomos* was significantly larger in several canine and premolar dimensions while *N. larvatus* had significantly larger molar dimensions. An additional 73 measurements were selected to represent occluding dental structures and a morphological integration analysis was conducted. Results of this analysis indicated that *C. polykomos* possessed a C¹-PM₃ complex which was more highly intercorrelated whereas the broad lophed *N. larvatus* molars constituted a more highly correlated functional unit.

It was suggested that the above differences between these two groups of leaf-eating monkeys probably resulted from inbreeding, isolation and drift.

1. Introduction

During the past several years a number of investigations have appeared which were addressed specifically to the problem of nonhuman Primate dental variability (Hooijer, 1948; Ashton & Zuckerman, 1950; Schuman & Brace, 1955; Freedman, 1957; Ockerse, 1959; Swindler, Gavan & Turner, 1963; Frisch, 1965; Saheki, 1966; Biggerstaff, 1966; Leutenegger, 1971). These studies have supplied the student of Primate odontology with valuable data concerning the morphological and metrical variability obtaining in the dentitions of living nonhuman Primates. Knowledge of the magnitude of this dental variability in different Primate species is a prerequisite for understanding the extent and kinds of dental variations occurring today within-and-between the various taxa. We hasten to add, that such information is also important to the paleoanthropologist studying the fossil antecedents of these same living forms. For an excellent statement of the value of dental variability studies for interpreting primate evolution the reader is referred to Frisch (1968).

Systematic studies of the dentitions of living nonhuman Primates also afford valuable data for investigating genetic and developmental problems. In a study of human lower first premolars Kraus & Furr (1953) demonstrated the necessity for having precise definitions of dental traits as a prelude to genetic analysis. It is well known that continuous traits such as the hypoconulid, expression of the lingual cusp of the lower fourth premolar and the size of the lingual cusp of the upper third premolar are quite variable from species to species. Such traits, and there are many others, are also considered meristic (repeated), i.e. they display gradients of expressivity in size and form in a tooth

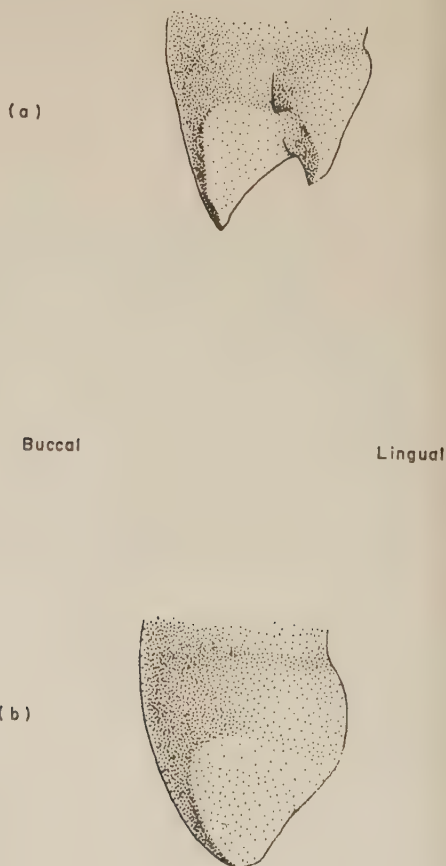
series. Since structural plasticity is evidenced by these dental characteristics we must exercise due caution in defining them. Once defined, their exact occurrence must be charted in adequate samples for each Primate species, and preferably for breeding populations within the species. For it will be then, and only then that we will be able to understand the complex nature of the Primate dentition.

The present paper is a comparative study of the dental morphology of *Colobus polykomos* and *Nasalis larvatus*. Both genera belong to the subfamily Colobinae and are arboreal, leaf-eating Old World monkeys. It might be assumed that these closely related, ethologically similar monkeys possess similar dental morphology. To test this hypothesis the morphologic and metric parameters of variation within each group were delineated, followed by statistical analysis to detect any possible differences between these two genera.

2. Materials and Methods

The morphological observations and odontometrics presented in this paper were made on dental casts taken from monkey skulls collected in Africa and Asia. The impressions were made with alginate and the casts were poured using a white dental stone. All casts were made within 5 minutes of the time the impressions were taken which minimizes

Figure 1. Left maxillary third premolar. Distal surface.



the possibility of any dimensional change. In an earlier study it was demonstrated that observations and measurements made on dental casts are comparable to those made on the original teeth (Swindler, Gavan & Turner, 1963).

All specimens were collected by expeditions from the Smithsonian Institution. *C. polykomos* came from Kenya and Uganda while *N. larvatus* was collected in West and Southeastern Borneo.

Bilateral observations were made but since dissimilarities between antimeres were seldom encountered, the sample sizes (N) were based on the number of specimens rather than on the number of teeth examined. Observations were limited to relatively unworn teeth and the following morphologic traits were investigated.

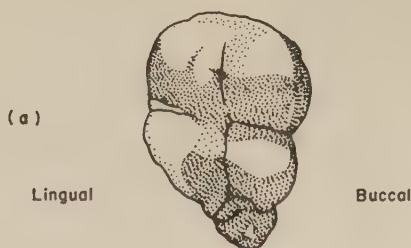
Total number of cusps

In an earlier paper, Hornbeck & Swindler (1967) defined a cusp as a tooth structure having a functional occlusal areal component delimited by developmental grooves and possessing an independent apex. This definition was used in this study. The number of cusps have been recorded for PM^3 (Figure 1).

Distal cusp on M^3

An extra cusp was occasionally observed on the distal marginal ridge of M^3 . If present it was buccal, lingual or central depending upon its position with reference to the long axis of the tooth (Figure 2). Saheki (1966) called this accessory cusp the distoconulus.

Figure 2. Left maxillary third molar showing distal cusp. (a) Occlusal surface, (b) lingual surface.



Size of the lingual cusp on PM₄

The expression of the lingual cusp was categorized as absent, small, large and greater than the buccal cusp (Figure 3).

Relative position of the lingual cusp on PM₄

The lingual cusp was opposite or distal to the buccal cusp (Figure 4).

Position of Hypoconulid on M₃

The hypoconulid was either buccal or central, that is, the mass of the cusp was equally distributed on either side of a line drawn through the long axis of the tooth, or it was

Figure 3. Right mandibular fourth premolar showing expression of lingual cusp. (a) Absent, (b) small, (c) large.

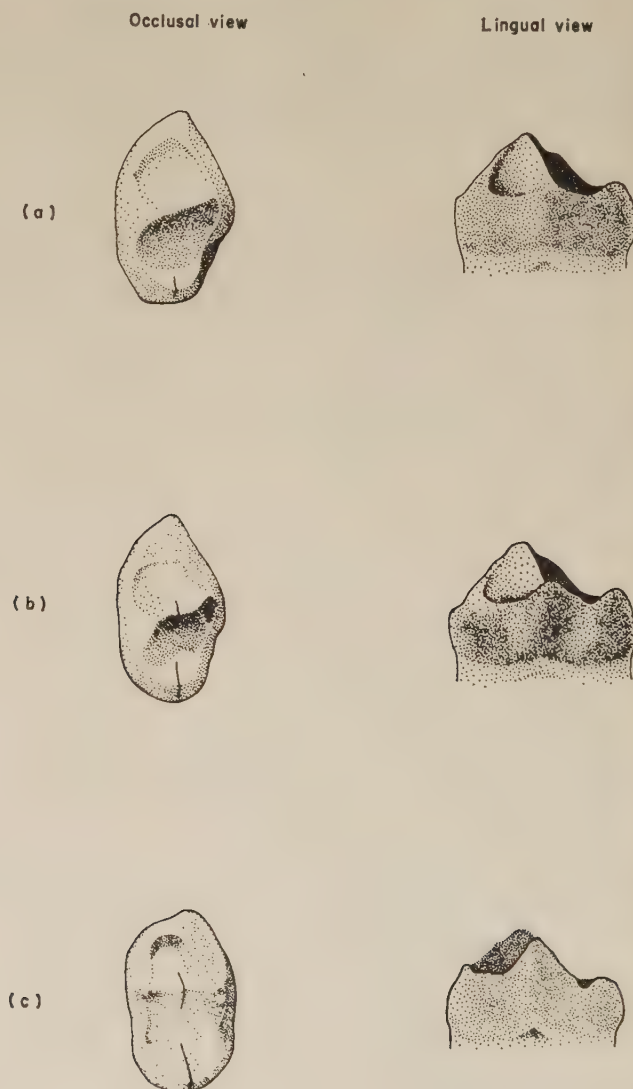
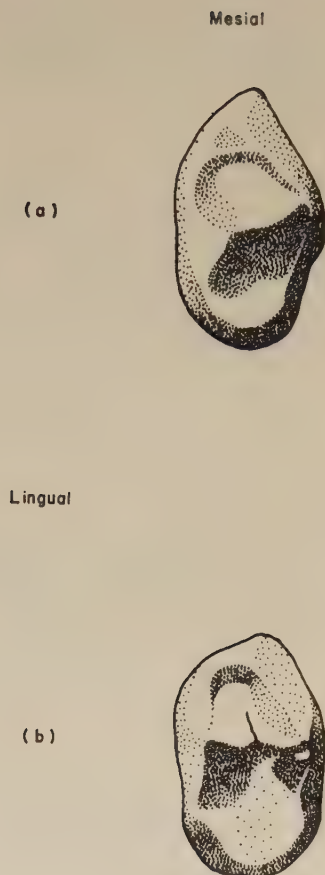


Figure 4. Occlusal view of right mandibular fourth premolar showing position of lingual cusp. (a) distal, (b) opposite.



positioned buccally to this line. We have followed Frisch (1965) in defining the position of the hypoconulid (Figure 5).

Tuberculum sextum (*sixth cusp*) on M_3

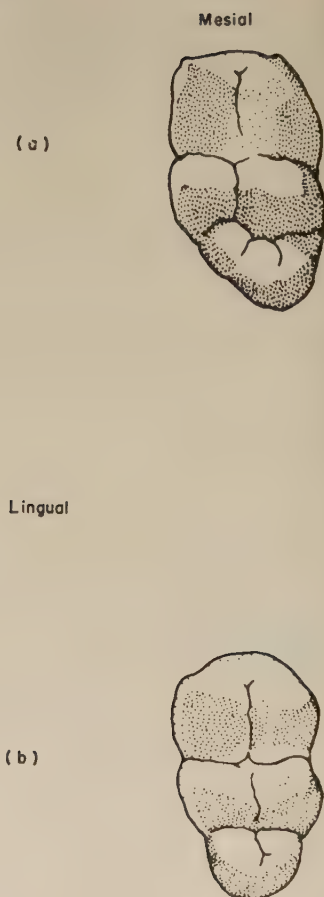
An extra cusp of varying size insinuated between the hypoconulid and the entoconid. In the present sample it was observed only on molars having 5 cusps (Figure 6).

The chi-square statistic was performed to test the null hypothesis of equal trait distributions between sexes and species.

Samples of *C. polykomos* (24 males, 23 females) and *N. larvatus* (23 males, 14 females) were selected for metric analysis. Limited wear was the sole criterion for drawing samples of the two taxa. This procedure was employed to reduce the possibility of measurement error due to occlusal or approximal wear.

Mesiodistal and buccolingual metric estimates were taken of the upper canine and all postcanine teeth. Standard odontometric procedures were followed (Swindler, Gavan & Turner, 1963). Due to the sectorial nature of PM_3 the mesiodistal dimension was taken from the mesial marginal ridge to the distal surface of the tooth. Measurements were taken of the right upper and lower dentition with occasional substitution of left side measurements when right side estimates were not possible. All measurements were

Figure 5. Occlusal view of right mandibular third molar showing position of hypoconulid. (a) Buccal, (b) central.



made to the nearest 0.1 mm with a Boley gauge. Repeated measurements of 5 specimens chosen at random showed an average difference of 0.13 mm for estimates of gross tooth dimensions and 0.15 mm for detailed crown measurements.

In addition to the above 29 estimates, an additional 73 measurements were taken. Wear facet studies were conducted to determine which surfaces of the upper and lower teeth occluded with one another. The results of these observations were in agreement

Figure 6. Lingual-occlusal aspect of right mandibular third molar showing *tuberculum sextum*.

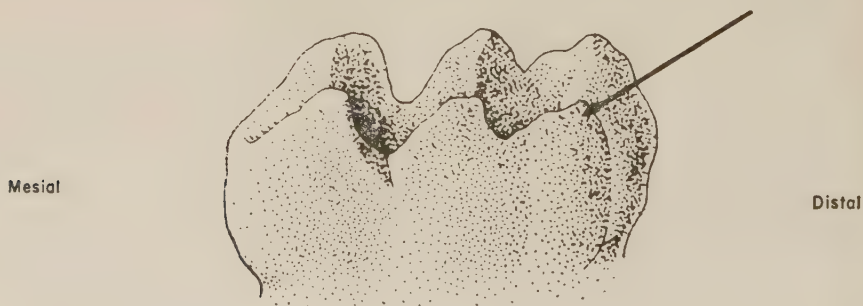
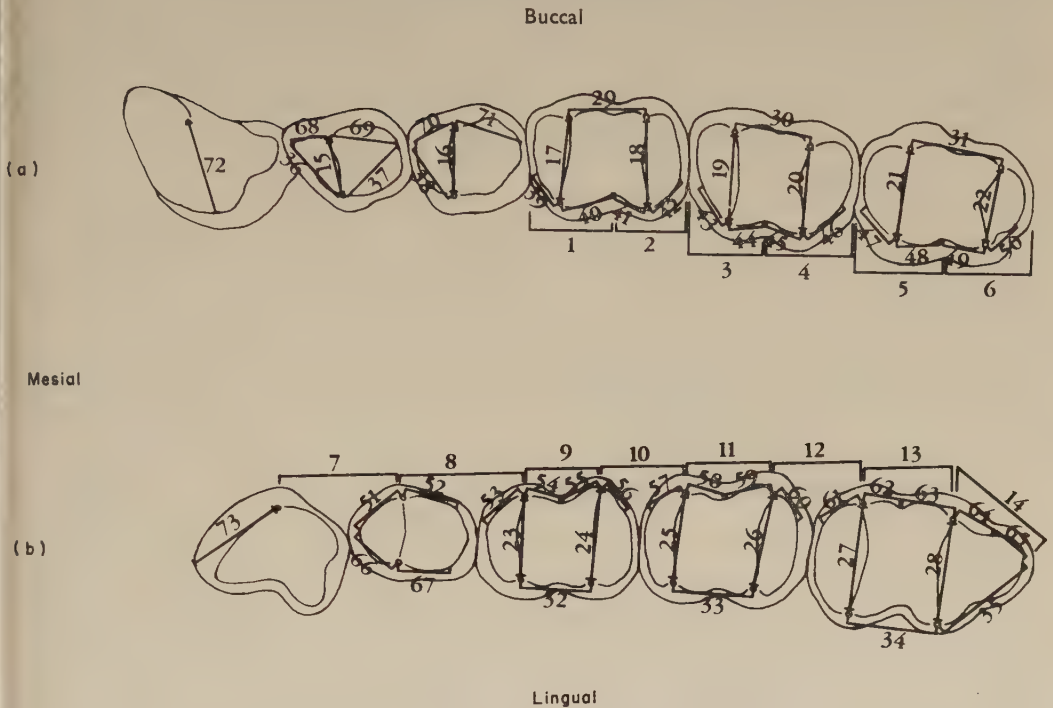


Figure 7. Schematic drawing of maxillary and mandibular Colobinae dentition showing 73 measures of occlusally important dental surfaces. (a) Maxillary, (b) mandibular.



with the wear facet information recorded by Mills (1955, 1963). Measures were then selected to represent the occlusally significant patterns. These 73 measurements were summarized in Figure 7.

Measurements 1 to 14 were mesiodistal estimates of the upper molar lingual cusps and the lower dental spaces through which the upper dental elements passed. Dimensions 15 to 28 represented the distance between the buccal and lingual cusps of the upper and lower dentitions. Measures 29 to 35 estimated the distance between the upper molar buccal cusps as well as between the lower molar lingual cusps. Estimates 36 to 71 were of the distance from marginal ridges and developmental grooves to cusp apices on the postcanine teeth. Measure 72 represented the height of the upper canine taken from the lingual cemento-enamel junction to the apex of the crown and measure 73 estimated the crest length of PM₃ taken from the cusp apex to the mesial crest termination.

All metric estimates were keypunched and verified to allow for computer analysis. With the aid of the University of Washington's CDC 6000, basic statistics were calculated on all variables. These included the mean, range, variance, standard deviation and standard error of the mean. Hypotheses of equality of means between sexes of each species and between both taxa by sex were tested using the appropriate small sample *t*-test statistic (Sokal & Rohlf, 1969). *F*-tests were likewise performed on the same groups to test for the equivalence of variances. In several cases, the resulting *F*-statistic revealed significant differences between variances. In all such cases the approximated *t*-values were calculated using the appropriate *t* statistic and critical value (Sokal & Rohlf, 1969, p. 374).

Pearsonian correlations were calculated between all 102 metric estimates of each sex of each species. These correlations were then examined following the general procedure of Olson & Miller (1951, 1958). The statistic I_e defined by Olson and Miller was modified by I_r as stated below and used to estimate the level of 'morphological integration' within teeth and dental series. The usage of r rather than the theoretical value e was used to avoid the difficulties mentioned by critics of Olson and Miller's procedure (Bock, 1960; Van Valen, 1965). I_r was defined as:

$$I_r = \frac{4(B_r)^2}{K_r(n^2 - n)^2} \quad \text{when } B_r \geq 1,$$

$$I_r = 0 \quad \text{when } B_r = 0$$

and where:

n = The number of measurements.

B_r = The number of correlated (bonded) measurements evaluated for a selected value of r for a suite of measurements.

K_r = The number of intercorrelated measurements formed in which all contained measures were intercorrelated one with every other and evaluated at a selected value of r .

[Modified from Olson & Miller (1958).]

3. Results and Discussion

General

The two genera studied in this paper belong to the subfamily Colobinae and for the most part are arboreal, leaf-eating Old World monkeys. The Colobinae have apparently been separated from the other subfamily of Old World monkeys, the Cercopithecinae, since the Miocene (Pilbeam & Walker, 1968; Simons, 1969). They are distinguished anatomically by the absence of cheek pouches, reduced thumbs and the presence of an elaborate sacculated stomach. The several genera are distributed over Malaysia, parts of China, the southern slopes of the Himalayas, and *Colobus* represents the only African member of the group. Their locomotor behaviour is classified as semibrachiation and most species of the subfamily spend the majority of their time in the trees, although *Presbytis entellus* (Hanuman langur) may spend upwards of 60% of their day on the ground (Napier & Napier, 1967).

The proboscis monkey (*N. larvatus*) is restricted in its distribution to Borneo where it inhabits the forest and mangrove swamps. During the day it prefers the mangrove, while at night it retreats to the tall pedada trees which afford protection from predators (Kern, 1964). The troop consists of approximately 20 individuals whose home range occupies a little over one-half mile per group and according to Kern (1964), there was no evidence that the proboscis monkey ever establishes a territory and defends it. In a recent study by Kawabe & Mano (1972) intratroup organization was shown to be highly structured and interestingly, these authors noted a strong terrestrial tendency for the proboscis monkey. It is estimated that at least 95% of the diet of the proboscis monkey consists of leaves, while the remaining 5% is made up of fruits and flowers (Kern, 1964). The mangrove and pedada leaves are their favourite food and are usually eaten directly from the branch.

The Black and White Colobus (*C. polykomos*) is widely distributed throughout the high forest of lowland and montane Africa. It spends much of its time in the upper layers of the forest, rarely being observed lower than the middle layer. Troop size is said to vary widely among *Colobus* (6 to 20) with small home ranges (Booth, 1957). Indeed, what evidence there is suggests that arboreal species such as *Colobus* are found in small groups with circumscribed home ranges (Hall, 1968). On the other hand, these small bands defend their territories by a combination of pronounced vocal and physical display by the males (Napier & Napier, 1967). Their diet consists almost exclusively of leaves and Booth (1956) was unable to detect a particle of fruit or animal matter in the stomachs of 41 Black and White Colobus monkeys.

In summary, these two genera are representative of a group of monkeys which parted from the Cercopithecinae some 19 million years ago during the Miocene period. Indeed, Jolly (1966) and Napier & Napier (1967) believe that the earliest Old World monkeys were the Colobinae. The arboreal, leaf-eating econiche occupied by the living colobines is reflected in various ways by their anatomy and physiology. The different members of the subfamily share many characters in common, while displaying a certain degree of variability. The amount and kinds of dental variability is the immediate problem.

Morphology

Among the cercopithecoids the upper premolars were considered to be "typically bicuspid (Le Gros Clark, 1971). That is, each tooth possessed a buccal and lingual cusp of approximately equal size. The present findings would agree with this statement regarding PM⁴, not PM³. The latter tooth was found to be quite variable both within-and-between the two genera studied (Figure 1 and Table 1). The morphological variation displayed by this tooth ranged from a structure with a single, large buccal cusp to the more characteristic bicuspid form. The former tooth always possessed a well formed lingual cingulum and it was the degree of development of the cingulum that dictated the number of cusps. In the present study, a cingulum that had an areal component set off by developmental grooves and possessing a separate apex constituted a cusp and the tooth considered bicuspid (Figure 1).

The maxillary third premolar of *N. larvatus* usually had two cusps, while in *C. polykomos* it more often displayed a single cusp (Table 1). The generic difference between the distributions of this dental trait was significant at $P < 0.01$ (Table 8). The sexes were combined for this analysis even though there was a sex difference between the distributions of *C. polykomos*. This procedure was justified since a chi-square test between the sexes of the two species revealed a significant difference between their distributions. Interestingly, the females of both taxa showed a greater frequency of bicuspid maxillary

Table 1 Total number of cusps on PM³

Species	Sex	N	n	Number of cusps			
				1	2		
				%	n		%
<i>Colobus polykomos</i>	M	60	56	93.3	4		6.7
<i>Colobus polykomos</i>	F	37	28	75.7	9		24.3
<i>Nasalis larvatus</i>	M	26	3	11.5	23		88.5
<i>Nasalis larvatus</i>	F	15	0	0	15		100.0

Table 2 **Distal cusp on M³**

Species	Sex	N	Absent		Lingual		Central		Buccal	
			n	%	n	%	n	%	n	%
<i>Colobus polykomos</i>	M	58	45	77.6	4	6.9	1	1.7	8	13.4
<i>Colobus polykomos</i>	F	36	25	69.4	0	0	3	8.3	8	22.2
<i>Nasalis larvatus</i>	M	26	23	88.5	1	3.8	1	3.8	1	3.8
<i>Nasalis larvatus</i>	F	15	10	66.7	0	0	4	26.7	1	6.7

third premolars. Also it should be noted that both morphological varieties of premolar existed in each group even though there was a statistically significant difference between their distributions. One point seems clear, the *carte blanche* descriptions of bicuspid maxillary third premolars of colobines found in the literature are no longer tenable. These teeth blazon a degree of morphological variability not expected in 2 groups of monkeys so closely related and so similar in dietary habits.

The upper third molar had 4 cusps and was bilophodont in colobines as well as in all Old World monkeys. Occasionally a distal accessory cusp developed on the distal marginal ridge (Figure 2 and Table 2). In the present study it was more frequently located buccally in *C. polykomos* and centrally in *N. larvatus*. Saheki (1966) described two types in *Macaca*, buccal and lingual. The buccal cusp was more frequently observed in *Macaca fuscata yakui* (60%) than in *Macaca fuscata fuscata* (10.5%), and it often was of large size, even approximating the metacone. Indeed, Saheki felt that a large distobuccal cusp was a diagnostic feature of the subspecies, *M. f. yakui*.

In the present sample it was too infrequent to be of much taxonomic value and there was no significant difference between the distributions (presence or absence) of the trait intergenerically (Table 8). There was likewise, no significant sexual dimorphism within either group, although the females had a higher frequency of the distal cusp. It never approached the metacone in size and the largest distobuccal cusp observed is depicted in Figure 2. The distal cusp was never in articulation with the hypoconulid when in occlusion, rather it was positioned above and distal to this cusp. It thus plays little, if any, role in mastication even though it adds to the total mesiodistal dimension of the tooth. This is true, even in well worn upper molars.

The mandibular fourth premolar was considered to be a bicuspid tooth in the Cercopithecoidea (Le Gros Clark, 1971). Recently, however, Hornbeck & Swindler (1967) demonstrated that this is a complex tooth in living cercopithecoids and requires more intensive study before valid generalizations can be promulgated about its anatomy.

In *C. polykomos* PM₄ displayed three cusps in about 95% of the sample, while the remainder had two cusps (Figure 3 and Table 3). The 3 cusps included a buccal, lingual and a smaller distolingual cusp. The lingual and buccal cusps were connected by the

Table 3 **Total number of cusps on PM₄**

Species	Sex	N	Number of cusps					
			2	3	4			
			n	%	n	%	n	%
<i>Colobus polykomos</i>	M	60	3	5.0	57	95.0	0	0
<i>Colobus polykomos</i>	F	37	1	2.7	36	97.3	0	0
<i>Nasalis larvatus</i>	M	26	0	0	23	88.5	3	11.5
<i>Nasalis larvatus</i>	F	15	0	0	15	100.0	0	0

The position of the hypoconulid in relation to the entoconid and hypoconid was found to be quite variable among living cercopithecoids (Swindler, McCoy & Hornbeck 1967)

Species	Sex	N	Absent		Large		Small		Lingual > Buccal	
			n	%	n	%	n	%	n	%
<i>Colobus polykomos</i>	M	60	3	5.0	37	61.7	20	33.3	0	0
<i>Colobus polykomos</i>	F	37	2	5.4	26	70.3	9	24.3	0	0
<i>Nasalis larvatus</i>	M	26	0	0	21	80.8	1	3.8	4	15.4
<i>Nasalis larvatus</i>	F	15	0	0	13	86.7	0	0	2	13.3

Table 5 Position of lingual cusp on PM₁

Species	Sex	N	Absent		Distal		Opposite	
			n	%	n	%	n	%
<i>Colobus polykomos</i>	M	60	3	5.0	43	71.7	14	23.3
<i>Colobus polykomos</i>	F	37	2	5.4	34	91.9	1	2.7
<i>Nasalis larvatus</i>	M	26	0	0	2	7.7	24	92.3
<i>Nasalis larvatus</i>	F	15	0	0	1	6.7	14	93.3

and hylobatids (Frisch, 1963). In his study of the gibbons, Frisch (1963) was able to clearly demonstrate a buccal shift in the position of the hypoconulid from the first to the third molar. Of course when working with Old World monkeys one is limited to M₃, since the cusp in question is normally only present on that tooth. The position of the hypoconulid in the present sample was either central or buccal (Figure 5). Their frequencies are presented in Table 6 and their chi-squares in Table 8. There was no sexual

Table 6 Position of hypoconulid on M₃

Species	Sex	N	Absent		Buccal		Central	
			n	%	n	%	n	%
<i>Colobus polykomos</i>	M	58	1	1.7	32	55.1	25	43.1
<i>Colobus polykomos</i>	F	36	0	0	19	52.8	17	47.2
<i>Nasalis larvatus</i>	M	26	1	3.8	16	61.5	9	34.6
<i>Nasalis larvatus</i>	F	15	0	0	9	60.0	6	40.0

dimorphism within either species, nor was there any significant difference between the two groups. Thus, the central or buccal hypoconulid appeared with approximately equal frequency in the present study. Indeed, a linguallly positioned hypoconulid is apparently a rare commodity among living cercopithecoids since it has been reported in only 3% of a sample of 57 baboons (*Papio anubis*) (Swindler, McCoy & Hornbeck, 1967). Frisch (1963) noted a lingual hypoconulid on all 3 molars of the gibbon, but it occurred on the third molar only twice in 62 animals.

Before leaving this interesting structure it should be mentioned that the size of the hypoconulid was markedly variable in both taxa studied as it was in previous investigations. It varied from complete absence to a well formed cusp occupying the greater part (width) of the distal surface of the tooth [Figure 5(b)]. Although no attempt was made to quantify this cusp in the present study, such an investigation should be undertaken, especially since Primate paleontologists are, in our opinion, mistakenly using the size of the hypoconulid for taxonomic and phylogenetic reconstructions (Simons, 1970).

The last dental trait to be considered is the *tuberculum sextum* or sixth cusp (Figure 6 and Table 7). The variability of the sixth cusp among Primates is well known, although

Table 7 Tuberculum sextum on M₃

Species	Sex	N	Absent		Present	
			n	%	n	%
<i>Colobus polykomos</i>	M	57	21	36.8	36	63.2
<i>Colobus polykomos</i>	F	36	14	38.9	22	61.1
<i>Nasalis larvatus</i>	M	25	15	60.0	10	40.0
<i>Nasalis larvatus</i>	F	15	10	66.7	5	33.3

Table 8

Chi-square tests

Species		Trait	Level of significance		
			0.01	0.05	N.S.
<i>Colobus polykomos</i>	M:F	PM ³ number		6.15	
<i>Nasalis larvatus</i>	M:F	of cusps			0.446
<i>C. polykomos</i> : <i>N. larvatus</i>		1 or 2	21.08		
<i>Colobus polykomos</i>	M:F	M ³ distal			0.774
<i>Nasalis larvatus</i>	M:F	cusp present			2.880
<i>C. polykomos</i> : <i>N. larvatus</i>		or absent			0.572
<i>Colobus polykomos</i>	M:F	PM ₄ number			0.306
<i>Nasalis larvatus</i>	M:F	of cusps 2			0.310
<i>C. polykomos</i> : <i>N. larvatus</i>		or 3			0.656
<i>Colobus polykomos</i>	M:F	PM ₄ size of			0.883
<i>Nasalis larvatus</i>	M:F	lingual cusp			0.263
<i>C. polykomos</i> : <i>N. larvatus</i>		large or small	13.73		
<i>Colobus polykomos</i>	M:F	PM ₄ position of	7.49		
<i>Nasalis larvatus</i>	M:F	lingual cusp			0.015
<i>C. polykomos</i> : <i>N. larvatus</i>		distal or opposite	69.02		
<i>Colobus polykomos</i>	M:F	M ₃ position of			0.101
<i>Nasalis larvatus</i>	M:F	hypoconulid buccal			0.060
<i>C. polykomos</i> : <i>N. larvatus</i>		or central			0.670
<i>Colobus polykomos</i>	M:F	M ₃ tuberculum			0.039
<i>Nasalis larvatus</i>	M:F	sextum present or			0.018
<i>C. polykomos</i> : <i>N. larvatus</i>		absent	6.98		

few investigators have done more than mention its presence or absence (Bennjeant, 1936; Remane, 1960; Saheki, 1966; Swindler, McCoy & Hornbeck, 1967). Hooijer (1962) stated that the sixth cusp occurred more often in large than in small M₃, however, in the present study such a correlation was not discovered. In Old World monkeys the sixth cusp had a frequency ranging from 11 % in *Cercopithecus albigena* (Swindler, McCoy & Hornbeck, 1967) to 96 % in *Macaca fuscata yakui* (Saheki, 1966). Of course, many species have not been systematically studied for the trait, but nevertheless, it seems clear that the sixth cusp enjoys a wide range of expression among the cercopithecoids.

The present data are presented in Tables 7 and 8. The sixth cusp was approximately twice as common in *C. polykomos* which was reflected by the high chi-square for the intergeneric difference between the distributions (Table 8). No sexual dimorphism was present.

The frequency of the presence of the sixth cusp (*c.* 36 %) in the present *N. larvatus* sample was much higher than the 7–10 % reported by Groves (1970) for the genus. He did not specify which, or how many monkeys of the two species *larvatus* and *concolor* contributed to the finding. In view of the obvious variability of the trait in Primates the discrepancy may reside at the species level, that is, it can be rather hazardous to utilize such highly variable characteristics in the definition of a genus before delineating the parameters of variability often separating closely related species.

In summary, the several dental traits studied above should make it abundantly clear how important it is to define and estimate the morphological boundaries of specific traits within-and-between taxa. One wonders how two such morphologically different teeth as the single and double cusped upper third premolars might be interpreted if found separately in the same fossil deposit.

Odontometrics

Sexual Dimorphism. The statistics for mesiodistal and buccolingual measurements for both *C. polykomos* and *N. larvatus* are presented in Tables 9 and 10. Comparisons with

Table 9 Maxillary tooth dimensions and *t*-values for sexual equality of means for *Colobus polykomos* and *Nasalis larvatus*

Tooth	Measure	Sex	Sample	<i>Colobus polykomos</i>			Sample	<i>Nasalis larvatus</i>		
				Mean	S.D.	<i>t</i> -value		Mean	S.D.	<i>t</i> -value
C ¹	MD	M	18	9.10	1.02	6.8**	21	8.66	0.51	15.4**
		F	22	7.30	0.65	(5.6††)	14	6.29	0.33	
PM ³	MD	M	24	5.24	0.47	1.7	23	5.28	0.31	3.8**
		F	23	5.03	0.34		14	4.90	0.27	
PM ⁴	MD	M	24	4.99	0.38	1.6	23	4.92	0.30	2.3*
		F	23	4.84	0.23	(0.59)	14	4.69	0.29	
M ¹	MD	M	24	7.01	0.40	2.8**	23	7.16	0.32	2.3**
		F	23	6.71	0.35		14	6.92	0.25	
M ²	MD	M	24	7.57	0.47	2.6**	23	8.09	0.38	3.7**
		F	23	7.25	0.35		14	7.61	0.40	
M ³	MD	M	24	7.58	0.45	0.8	23	7.80	0.46	2.0
		F	23	7.47	0.46		14	7.52	0.31	
C ¹	BL	M	21	6.48	0.50	6.6**	23	6.68	0.47	12.6**
		F	22	5.34	0.62		14	4.88	0.31	
PM ³	BL	M	24	5.67	0.56	2.7*	23	5.91	0.27	5.0**
		F	23	5.30	0.37	(2.66††)	14	5.44	0.28	
PM ⁴	BL	M	21	6.60	0.68	1.6	23	6.11	0.27	2.9**
		F	22	6.33	0.46	(1.62)	14	5.82	0.33	
M ^{1a}	BL	M	24	6.47	0.38	3.1**	23	6.26	0.16	4.1**
		F	23	6.11	0.41		14	5.96	0.29	(3.62††)
M ^{1b}	BL	M	24	6.20	0.40	2.7**	23	6.34	0.19	3.7**
		F	23	5.87	0.44		14	6.05	0.29	(3.33††)
M ^{2a}	BL	M	24	7.27	0.54	2.3**	23	7.29	0.24	4.9**
		F	23	6.94	0.44		14	6.87	0.26	
M ^{2b}	BL	M	24	6.83	0.51	2.7**	23	6.93	0.32	3.7**
		F	23	6.45	0.47		14	6.53	0.32	
M ^{3a}	BL	M	24	6.85	0.51	2.6**	23	7.15	0.28	5.0**
		F	23	6.51	0.40		14	6.71	0.24	
M ^{3b}	BL	M	24	6.28	0.72	2.3**	23	6.30	0.41	3.4**
		F	23	5.85	0.53		14	7.86	0.31	

*,** Significant *t*-value at $P < 0.05$ and $P < 0.01$ respectively; equal variance statistic.

†,†† Significant *t*-value at $P < 0.05$ and $P < 0.01$ respectively; unequal variance statistic. MD = Mesiodistal; BL = Buccolingual.

unequal variances are indicated by the placement of the estimated *t*-values in parentheses below the uncorrected *t*-values.

In general, significant differences were evident in both groups and in all cases the males were larger than females. With respect to the maxillary teeth, significant differences were noted in all comparisons except for: the M³ mesiodistal measurement of both species; both measures of PM⁴ in *C. polykomos*; and the mesiodistal diameter of PM³ in *C. polykomos*. Significant differences were observed in the mandibular dentitions in all mesiodistal measures of both taxa. Buccolingual comparisons revealed differences in all *N. larvatus* measurements except for: PM₄; M₂ and M₃ trigonids; and the talonid of M₃. The talonid of M₁ was the only buccolingual measurement not showing significant

Table 10

Mandibular tooth dimensions and *t*-values for sexual equality of means for *Colobus polykomos* and *Nasalis larvatus*

Tooth	Measure	Sex	Sample	<i>Colobus polykomos</i>			Sample	<i>Nasalis larvatus</i>		
				Mean	S.D.	<i>t</i> -value		Mean	S.D.	<i>t</i> -value
PM ₃	MD	M	24	7.09	0.56	5.4**	23	6.83	0.45	8.3**
		F	23	6.33	0.39	(5.5††)	14	5.62	0.39	
PM ₄	MD	M	24	6.04	0.46	3.6**	23	5.42	0.33	4.0**
		F	23	5.62	0.32	(3.61††)	14	5.00	0.29	
M ₁	MD	M	24	7.13	0.36	3.3**	23	7.32	0.30	3.7**
		F	23	6.80	0.32		14	6.93	0.32	
M ₂	MD	M	24	7.70	0.47	3.7**	23	8.19	0.28	4.9**
		F	23	7.25	0.34		14	7.68	0.34	
M ₃	MD	M	24	9.53	0.72	2.0**	23	10.26	0.54	3.3**
		F	23	9.16	0.51		14	9.68	0.51	
PM ₃	BL	M	24	4.80	0.55	3.6**	23	5.57	1.14	3.11**
		F	23	4.32	0.31	(3.67††)	14	4.59	0.44	(3.70††)
PM ₄	BL	M	24	4.72	0.49	3.0**	23	4.70	0.22	1.9
		F	23	4.35	0.35		14	4.54	0.33	
M _{1a}	BL	M	24	5.27	0.42	2.2*	23	5.18	0.20	2.2*
		F	23	5.00	0.40		14	5.01	0.27	
M _{1b}	BL	M	24	5.54	0.42	1.9	23	5.75	0.32	2.9**
		F	23	5.33	0.35		14	5.46	0.25	
M _{2a}	BL	M	24	6.27	0.61	2.3*	23	6.39	0.29	1.1
		F	23	5.90	0.45		14	6.29	0.27	
M _{2b}	BL	M	24	6.40	0.54	2.0*	23	6.60	0.28	3.2**
		F	23	6.11	0.44		14	6.29	0.30	
M _{3a}	BL	M	24	6.27	0.52	2.8**	23	6.63	0.32	1.5
		F	23	5.85	0.49		14	6.46	0.34	
M _{3b}	BL	M	24	6.10	0.49	2.2**	23	6.33	0.37	1.6
		F	23	5.81	0.36		14	6.13	0.39	

*,** Significant *t*-value at $P < 0.05$ and $P < 0.01$ respectively; equal variance statistic.

†,†† Significant *t*-value at $P < 0.05$ and $P < 0.01$ respectively; unequal variance statistic. MD = Mesiodistal; BL = Buccolingual.

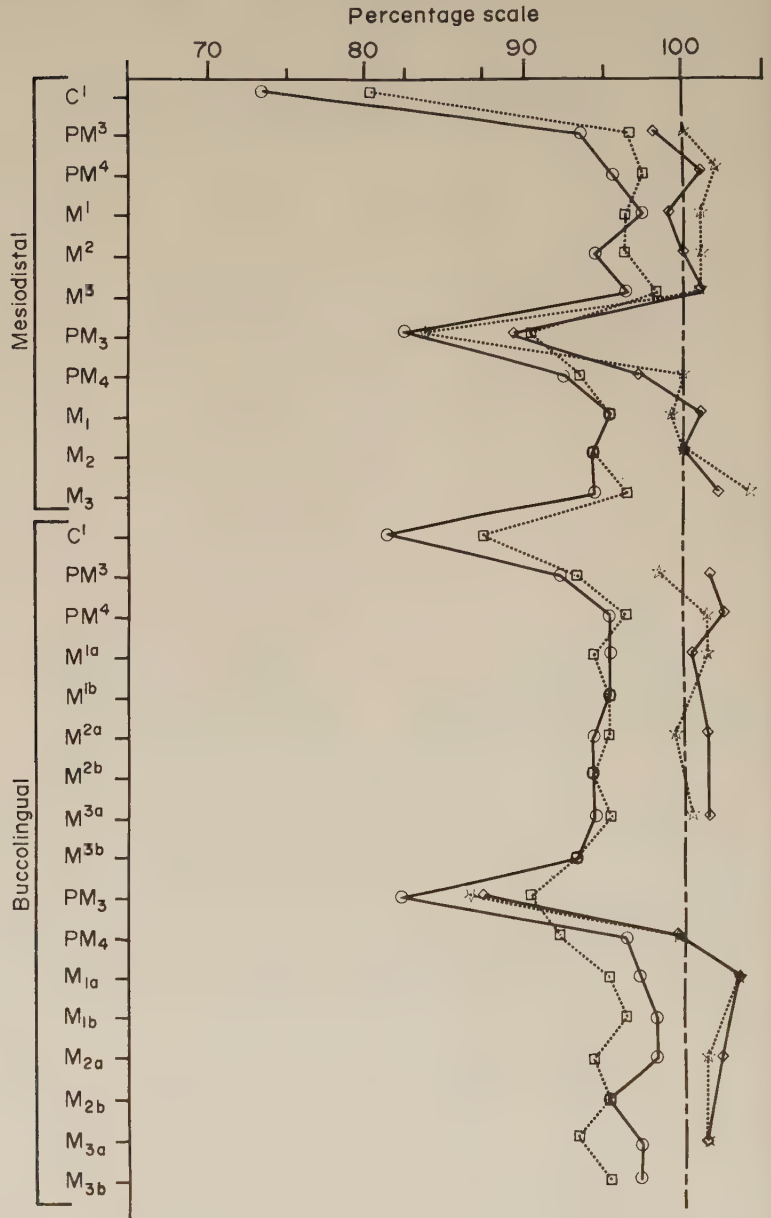
differences in *C. polykomos*. In view of the sexual differences in both taxa, the two sexes were considered separately for the remainder of the study.

To aid the reader in further comparisons, Figure 8 was prepared in which females were presented as a percentage of males. Calculations were based on estimates of means presented in Tables 9 and 10. Comparing the differences in percentages in Figure 8, or comparing differences of *t*-values between the two taxa, gave a good indication of the similarities and differences in the intensity of sexual dimorphism in the two taxa under consideration. The degree of sexual dimorphism was not constant within upper and lower dental series of both taxa. The pattern of sexual dimorphism, however, was the same in both groups as evidenced by peaks of dimorphic intensity in C¹ and PM₃ as well as by less significant differences in the upper postcanine and lower molar teeth.

Comparison of the intensities between the two groups under study revealed that differences in *t*-values, or in percentage points in Figure 8, were highest in C¹ and PM₃. *N. larvatus* greatly exceeded *C. polykomos* in the upper canine-lower third premolar complex whereas the differences diminished in the upper and lower premolars and molars. Indeed, *C. polykomos* showed equal or greater *t*-values in 4 buccolingual measures of the lower molars, one mesiodistal dimension of M¹, and buccolingual diameters of PM₃ and PM₄.

It has been shown for *Homo sapiens* that sexual dimorphism in tooth size was positively correlated with sexual dimorphism in body size and it was hypothesized by the same

Figure 8. Ratio diagram showing sexual dimorphism in tooth measurements Means of females expressed as percentages of males. a, Mesial moiety; b, distal moiety. ○, *Nasalis larvatus*; □, *Colobus polykomos*; ◇, *Procoobus badius*; ⚡, *Procolobus verus*.



authors that a similar correlation might characterize all higher Primates (Garn *et al.*, 1967). The present evidence does not support such a contention with regard to leaf-eating Old World monkeys. *N. larvatus* demonstrates much greater sexual dimorphism in body size than does *C. polykomos* (Napier & Napier, 1967). If sexual dimorphism in tooth size corresponds to dimorphism in body size, one would expect a rather uniformly

more intense tooth dimorphism in *N. larvatus*. This was not observed, however, in the results mentioned above. Included in Figure 8 are data on measures of *Procolobus badius* and *Procolobus verus* postcanine teeth (Leutenegger, 1971). Both of these species showed relatively little sexual dimorphism in body size (Napier & Napier, 1967). As can be seen in Figure 8, there was a corresponding reduction in sexual dimorphism in the molars but, in both measures of PM_3 , these species exceeded *C. polykomos* and approached *N. larvatus* in the intensity of sexual dimorphism. Impressive too was the high sexual dimorphism exhibited by *P. verus* for PM_3 since in this species females tend to have a larger body size than males (Napier & Napier, 1967). The discrepancies involving PM_3 are even more revealing since it was in this tooth that the greatest correspondence between tooth size dimorphism and body size dimorphism was found in *Homo sapiens* (Garn *et al.*, 1967). In conclusion, there seems to be no simple rule relating body size sexual dimorphism and tooth size dimorphism among the leaf-eating Old World monkeys.

Interspecies differences. The *t*-values for significant differences by sex between *N. larvatus* and *C. polykomos* are summarized in Table 11. The means of *N. larvatus* as a percentage of the means of *C. polykomos* by sex are graphically illustrated in Figure 9. As can be seen, both sexes exhibited similar contrasts between the two taxa. Major discrepancies

Table 11 Resulting *t*-values from comparisons of *Colobus polykomos* and *Nasalis larvatus* by sex

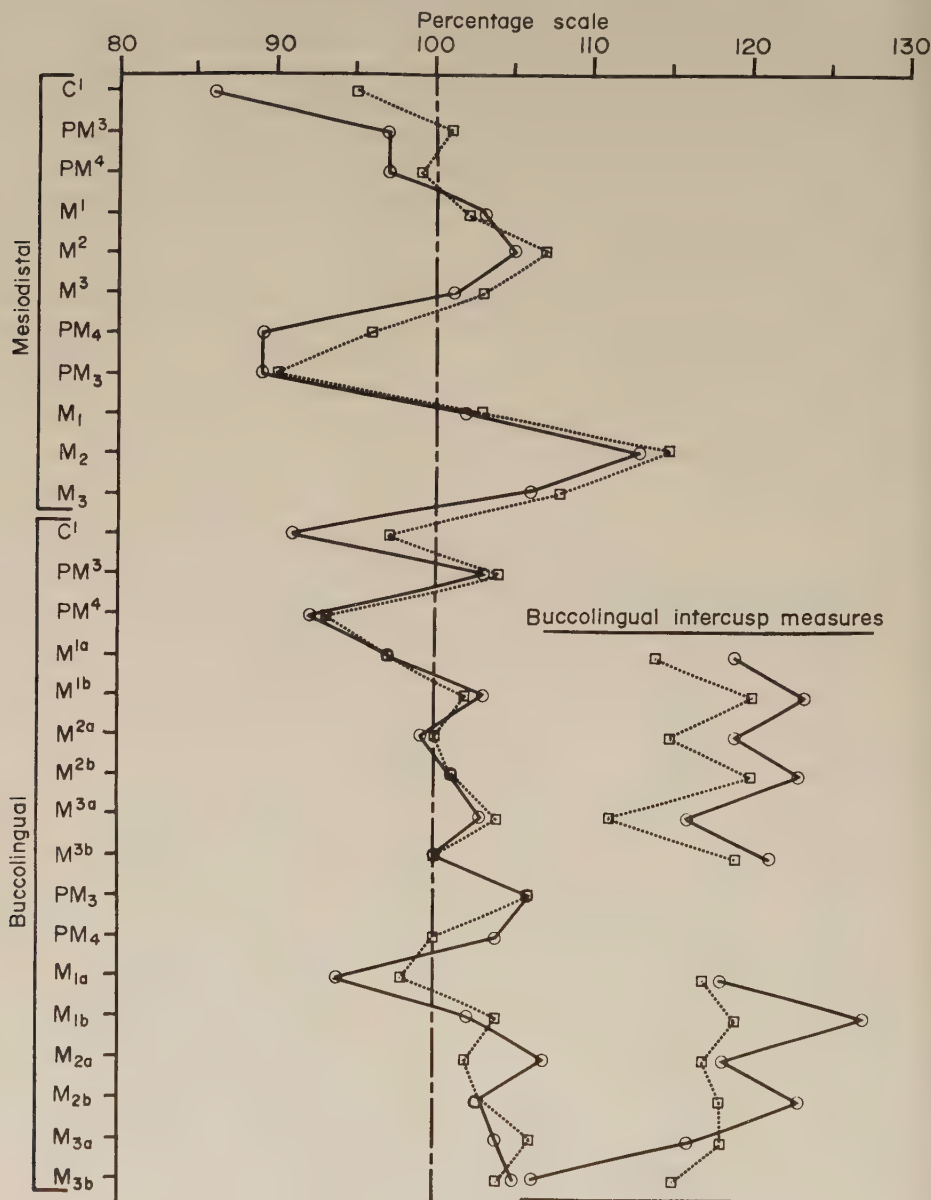
Tooth	Measure	Male ^a	Female ^a	Tooth	Measure	Male ^a	Female ^a
C ¹	MD	1.8 (1.6)	5.4** (6.22††)	PM ₃	MD	1.8	5.4**
PM ³	MD	-0.4 (-0.86)	1.2	PM ₄	MD	5.2**	5.9**
PM ⁴	MD	0.7	1.8	M ₁	MD	-2.0	-1.2
M ¹	MD	-1.4	-2.0	M ₂	MD	-4.3** (-4.34††)	-3.6**
M ²	MD	-4.1**	-2.8**	M ₃	MD	-3.9**	-3.0**
M ³	MD	-1.6	-0.3	PM ₃	BL	-3.0** (-2.93††)	-2.1*
C ¹	BL	-1.4	2.5* (2.91††)	PM ₄	BL	0.2 (0.19)	-1.6
PM ³	BL	-1.8 (-1.8)	-1.2	M _{1a}	BL	0.9 (0.93)	-0.1
PM ⁴	BL	3.2** (3.23)	3.6**	M _{1b}	BL	-1.9	-1.3
M ^{1a}	BL	2.5* (2.52)	1.2	M _{2a}	BL	-0.9 (-0.87)	-2.9** (-3.21††)
M ^{1b}	BL	-1.6 (-1.59)	-1.4	M _{2b}	BL	-1.6 (-1.60)	-1.4
M ^{2a}	BL	-0.1 (-0.082)	0.5 (0.59)	M _{3a}	BL	-2.9** (-2.92††)	-4.1**
M ^{2b}	BL	-0.8 (-0.78)	-0.5	M _{3b}	BL	-1.9	-2.5**
M ^{3a}	BL	-2.5** (-2.5†)	-1.7 (-1.9)				
M ^{3b}	BL	-0.1 (-0.08)	-0.1 (-0.09)				

^a Positive *t*-values indicate *C. polykomos* > *N. larvatus*.

*, ** Significant *t*-value at *P* < 0.05 and *P* < 0.01 respectively; equal variance statistic.

†, †† Significant *t*-value at *P* < 0.05 and *P* < 0.01 respectively; unequal variance statistic. MD = Mesiodistal; BL = Buccolingual.

Figure 9. Ratio diagram showing means of *Nasalis larvatus* expressed as percentages of *Colobus polykomos* means. a, Mesial moiety, b, distal moiety. □, Male; ○, female.



occurred only with respect to the C¹-PM₃ complex. This was understandable in view of the much greater sexual dimorphism exhibited in this complex by *N. larvatus*.

It was observed that, with the exception of PM₃ and PM₄ estimates, *C. polykomos* exceeded *N. larvatus* in C¹, PM₃ and PM₄ dimensions. Upper third premolar buccolingual size increase in *N. larvatus* was due to increased development of lingual cusps on this tooth. On the other hand, *N. larvatus* tended to have larger molar dimensions,

with the exception of the M^1 buccolingual trigonid dimension. In 8 measures of M^2 and M^3 , differences significant at $P < 0.05$ were observed in at least 1 sex and in 4 such cases significant differences were observed in both sexes.

These results suggested a greater functional specialization in the canine-premolar complex for *C. polykomos* and/or an increased specialization of the molar complex for *N. larvatus*. The former is indicated in view of smaller body size, lower canine and premolar sexual dimorphism, yet greater canine-premolar absolute size in *C. polykomos*. The possibility of the latter is enhanced by study of the percentages in Figure 9 for the measurement between buccal and lingual apices of the molars. These measures (nos 17–28, Figure 7) represented the breadth of the lophs on the above teeth. (With the exception of the talonid measure of M_1 and M_2 in *C. polykomos*, there was no significant sexual dimorphism shown in any of these measures.) It is obvious from Figure 9 that *N. larvatus* had dramatically more open-faced molars resulting in broader lophs on all molars. All of the differences in loph dimensions were significant at $P < 0.01$.

The above contrasts in tooth size and morphology were suggestive of some kind of functional differences between *N. larvatus* and *C. polykomos*. It was queried whether or not the different morphologic and implied functional contrasts were associated with biformity of integration. In an attempt to reveal any such differences in patterning, a study of 'morphological integration' was undertaken. Following the logic of Olson & Miller (1958), functionally interrelated traits show higher intercorrelation, i.e. greater morphological integration, than do non-related characters. Thus, one would expect a relatively higher intercorrelation of occlusal measures associated with the upper canine-premolar region in *C. polykomos* if indeed, this species is relatively more specialized in this complex than is *N. larvatus*. Likewise, one would expect a relatively higher integration within and between dental measures involving the molars in *N. larvatus* if this group exhibits relatively more specialized molar morphology. Equal integration would indicate that morphological features of both groups are functionally organized to the same degree and that functional stresses do not differ between groups.

Morphological integration. The results of morphological integration analysis were presented by a *a priori* selection of measures representing functional units and examination of inter-correlations within such units. The results presented integration considerations of: (1) individual teeth; (2) teeth within the upper and lower series separately; and (3) functional units between the upper and lower jaws.

(1) Within Tooth Integration

The within tooth I_r values for *C. polykomos* and *N. larvatus* at $r \geq 0.50$ are summarized in Table 12. I_r must, of course, always be compared at constant values of r . Selecting this value of r assured that all comparisons of correlations were significant at $P < 0.05$. Comparison of I_r should also be made of units with comparable measures since the unintentional inclusion of poorly correlated estimates will drastically lower I_r values. Comparisons of this integration estimate were therefore made of premolars, one with the other, as well as of molars.

Integration of PM^3 , PM^4 and PM_4 was actually weak and I_r values for these teeth were deceptively high at $r \geq 0.50$. Since only 4 to 5 measures were involved, the only bond which was formed in each case frequently resulted in integration estimates higher than the more elaborately measured molars. In all cases the single bond present in the premolars was weak, less than $r \geq 0.70$, and five of the 12 bonds appeared only when

Table 12 I_r Values for within tooth correlations *

Genus	Species	Sex	PM ³	PM ⁴	M ¹	M ²	M ³	PM ⁴	M ¹	M ²	M ³	M ₂	M ₃	M ₃ + hypoconulid
<i>Colobus</i>	<i>polykomos</i>	(Male)	0.01000	0.02778	0.00231	0.01543	0.00154	0.02778	0.01228	0.02066	0.01629	0.00750	0.00138	0.00347
<i>Colobus</i>	<i>polykomos</i>	(Female)	0.01000	0.02778	0.00231	0.00945	0.00154	0.02778	0.00127	0.03871	0.00383	0.00797	0.00551	0.00750
<i>Nasalis</i>	<i>larvatus</i>	(Male)	0.01000	0.02778	0.00777	0.00231	0.00386	0.02778	0.00383	0.00510	0.00797	0.01560	0.00551	0.00750
<i>Nasalis</i>	<i>larvatus</i>	(Female)	0.01000	0.02778	0.00988	0.02608	0.00823	0.02778	0.00638	0.00510	0.01560	0.00551	0.00750	0.00750

* I_r Value for $r \geq 0.50$ only.

Table 13

 I_r Values for within dental series measures*

Genus	Species	Sex	Upper molar apex to groove (36-50)	Lower molar apex to groove (51-65)	Upper molar lophs (17-22)	Upper molar lophs + premolar (15-22)	Lower molar lophs (23-28)
<i>Colobus</i>	<i>polykomos</i>	(Male)	0.00150	0.00082	0.01778	0.00638	0.45351
<i>Colobus</i>	<i>polykomos</i>	(Female)	0.00018	0.00274	0.03704	0.03444	0.06859
<i>Nasalis</i>	<i>larvatus</i>	(Male)	0.00018	0.00116	0.07111	0.03593	0.14815
<i>Nasalis</i>	<i>larvatus</i>	(Female)	0.01061	0.00330	0.15926	0.14063	0.04592

* I_r Values for $r > 0.50$ only.

the correlation level was lowered to $r \geq 0.50$. All bonds involved one measure relating to the lingual cusps or its equivalent.

Comparison of individual molars revealed that female *N. larvatus* had higher I_r values than female *C. polykomos*, except for M_2 , but male *N. larvatus* showed lower values than male *C. polykomos*, except for M^3 . In both sexes of both groups, addition of hypoconulid measures reduced I_r values.

Details of bonding within individual molars, however, were of interest. Within each of the upper first two molars, measures of the protocone and hypocone (nos 1-4, Figure 7) were correlated in both sexes of both groups. Measures 5 and 6 were bonded at $r \geq 0.70$ in *N. larvatus* but were unbonded at $r \geq 0.50$ in *C. polykomos*. Correlations between the mesial and distal lophs of the upper first molar were strong in *C. polykomos* ($r \geq 0.80$ females; $r \geq 0.70$ males) and weak ($r \geq 0.60$) to absent in female and male *N. larvatus* respectively. In the upper second and third molars, however, correlations between lophs of individual molars were strong in *N. larvatus* and completely absent in *C. polykomos* (at $r \geq 0.50$). Correlations between lophs were present in all lower molars of both groups.

(2) Correlations Within Upper and Lower Dental Arches.

The I_r values for intercorrelations within arches involving buccolingual crests and cusp-apex-to-groove measures are summarized in Table 13. The I_r value for the latter were uniformly low except for the upper arch measures of female *N. larvatus*. Bonding was low indeed for all groups, except again for female *N. larvatus*, since no bonds were formed above $r \geq 0.70$ and these were few in number and sporadic in distribution.

With respect to loph dimension (estimated by measures 1-28, Figure 7), I_r values were respectably high. *N. larvatus* had consistently higher values in the upper dental series, whereas the sexes of *C. polykomos* showed respectively higher values in the lower dentition. There were no distinguishing bonding patterns within the upper or lower molar series.

Included in Table 13 are the I_r values for upper molar lophs with the addition of upper premolar analogues (measures 15 and 16, Figure 7). As with the values for individual molars, *N. larvatus* showed higher I_r estimates than did *C. polykomos*. The bonding patterns likewise were of interest. Measure 15 (PM^3) was bonded to analogous measures of the fourth premolar and to the molars in both sexes of *N. larvatus*. In males the intercorrelated group 15-16-18 formed at $r \geq 0.50$ while in females the group 15-16-22 formed at $r \geq 0.70$ and the integrated group 15-16-19-20-21-22 at $r \geq 0.50$. Such bonding is completely absent in both sexes of *C. polykomos* (at $r \geq 0.50$).

(3) Upper to Lower Functional Unit Considerations

The I_r values for individual functional units are summarized in Table 14. For these evaluations, buccolingual and mesiodistal dimensions were included along with respective

Table 14 *I_r* Values for functional units between dental arches for each sex of each taxa*

Genus	Species	Sex	C ¹ -PM ₃	PM ³ -PM ₃ , PM ₄	PM ⁴ -PM ₄ , M ₁	M ¹ -M ₁ , M ₂	M ² -M ₂ , M ₃	M ³ -M ₃
<i>Colobus</i>	<i>polykomos</i>	(Male)	0.05444	0.00948	0.00175	0.00101	0.00384	0.00153
<i>Colobus</i>	<i>polykomos</i>	(Female)	0.14222	0.00207	0.00197	0.00231	0.00368	0.00070
<i>Nasalis</i>	<i>larvatus</i>	(Male)	0.00444	0.00099	0.00082	0.00026	0.00070	0.00144
<i>Nasalis</i>	<i>larvatus</i>	(Female)	0.05333	0.00463	0.01893	0.00155	0.00379	0.00151

* *I_r* Value for $r \geq 0.50$ only.

measures listed in Figure 7. *C. polykomos* showed consistently higher I_r values than did *N. larvatus* when the C^1 - PM_3 unit was examined. In both sexes of *C. polykomos*, C^1 -height was highly intercorrelated with mesiodistal and buccolingual measures of the same tooth. Such groupings were absent in both sexes of *N. larvatus*. Bonds between the mesiodistal measure of the upper canine with measures 72 and 73 were observed in male *C. polykomos* and the intercorrelated group of buccolingual measures of C^1 and PM_3 with measures 72 and 73 in female *C. polykomos*. Such groups were totally lacking for male *N. larvatus* although females of this species demonstrated the correlated group of 72, 73 and buccolingual of PM_3 . Within both species, females exhibited greater integration than males with respect to this complex.

Results of the premolar functional units were less informative than the above. In both cases, *C. polykomos* males had higher I_r values than *N. larvatus* males but females of the latter species exceeded females of *C. polykomos* in both functional units. Likewise, there were no uniform sexual tendencies within either group.

Gross size factors predominated within both sexes of both species with respect to the PM^3 - PM_3 , PM_4 functional unit. Likewise, gross size factors were of sole importance in the PM^4 - PM_4 , M_1 complex except for female *N. larvatus*. In female *N. larvatus*, extensive intercorrelations were revealed by the totally intercorrelated group 70-8-52-38-67 as well as groupings involving gross dimensions of PM^4 .

Neither species showed consistently higher I_r values for molar functional units. With the exception of *N. larvatus* males, highest I_r values were observed for the M^2 - M_2 , M_3 complex within the molar units. In *N. larvatus* males the M^3 - M_3 functional unit had the highest associated I_r value.

All 4 groups showed strong bonding involving buccolingual and upper to lower loph correlations within the M^1 - M_1 , M_2 complex. In the females of both species mesiodistal measures were included in the above intercorrelated groups.

With respect to the M^2 - M_2 , M_3 complex, all groups showed total intercorrelation of gross size measures. In addition, both sexes of *N. larvatus* demonstrated complete intercorrelation of upper and lower lophs. Such correlations were weak or absent in *C. polykomos*. Indeed female *C. polykomos* showed only one interloph correlation and males only 3 at $r \geq 0.50$.

As with the above unit, the M^3 - M_3 complex demonstrated good intercorrelation of gross size measures. Likewise, both sexes of *N. larvatus* showed very strong intercorrelation of lophs. Within *N. larvatus* complete intercorrelation was observed at $r \geq 0.70$ for females and at $r \geq 0.60$ in males. Comparable correlations were totally lacking in male *C. polykomos* and weak in females (4 bonds at $r \geq 0.50$).

Considering each tooth individually, it was realized that both groups demonstrated equally integrated premolars. In terms of general integration, both taxa likewise showed approximately equal I_r values within molars. Bonding patterns within the individual upper molars indicated that *N. larvatus* had greater correlation between lophs of the upper second and third molars than did *C. polykomos*.

Regarding intradental arch correlations, it was observed that both groups showed high intercorrelations of lophs within each dental arch. The bonding patterns involving PM^3 and PM^4 , however, indicated that in *N. larvatus* these teeth had been incorporated into the molar series whereas this had not occurred in *C. polykomos*.

The functional considerations regarding the upper canine and the premolars indicated that, with the relatively larger size of these teeth in *C. polykomos* there was a corresponding

increase in integration. The increase in integration, however, was limited to the C^1 -PM₃ functional complex. Although this increased integration implies a better efficiency within *C. polykomos* for this complex unit, it does not, of course explain the evolutionary mechanisms which resulted in the larger elements within *C. polykomos*. Interestingly, in both *N. larvatus* and *C. polykomos*, females consistently showed a much better integration within this complex than did males. Apparently, males of both groups evolved proportionally larger upper canines in spite of a general lowering of integration within this functional unit. This seems especially true for *N. larvatus* males. This suggests that, whatever selective pressures resulted in greater sexual dimorphism within this complex, they did not involve increased fitness due to a honning mechanism as has been suggested for baboons (Zingesser, 1969).

With respect to the molar functional complexes, it was observed that not only do *N. larvatus* monkeys have more open-faced molars with broader lophs, they also have a functionally better intercorrelated loph system. This, again, does not imply that increased integration resulted in the respective differences in morphology. To the contrary, the evolutionary steps leading to the broader lophs may have involved a temporary decrease in integration. But, in observing the present end products of such evolution, it can now be inferred that *N. larvatus* with its more openfaced molars and the corresponding increased loph integration is more specialized with respect to these morphological traits.

4. Summary

In order to determine the nature and extent of dental variability obtaining within-and-between two groups of monkeys belonging to the subfamily Colobinae the present investigation was carried out using a sample of 97 *C. polykomos* and 41 *N. larvatus*. The colobines were selected since they represent arboreal, leaf-eating monkeys who have presumably been occupying this econiche for some 19 million years and might, therefore, be expected to show similar dental adaptations.

There is a general similarity in the teeth of these two groups of monkeys, especially with respect to the relatively high pointed cusps of the molars which are separated by deep occlusal developmental grooves. Indeed, these deeply furrowed molars are the hallmark of the leaf-eater's dentition.

The distribution of other morphological traits showed differing frequencies within-and-between the two taxa. Thus, 4 of 7 traits were significantly different between the two genera. Two of these, the number of PM₃ cusps and the position of the lingual cusp on PM₄, resulted in highly contrasting forms between the two groups.

Metric comparisons between the two groups likewise revealed contrasting dental trends. *C. polykomos* exhibited a relatively specialized C^1 -PM₃ complex while *N. larvatus* demonstrated a relatively more open-faced molar complex with broad lophs. If genetic fields are viewed to simultaneously govern upper and lower occluding dental traits, the evolutionary mechanisms resulting in these contrasts might have been isolation and genetic drift. Alternatively, canine dimorphism and loph development may well have involved a degree of selection which increased frequencies of advantageous dental patterns in diverging groups of leaf-eaters. Thus, even slightly higher fitness values for particular traits could result in divergent trends over a several million year period.

Although the above pronounced intergeneric differences were not anticipated, equally instructive was the degree of intraspecific plasticity evidenced by the dental traits. Due

caution must therefore be employed when such variable traits are used in neontological or paleontological taxonomy.

When traits have no apparent occlusal significance it is difficult to explain such nuances of morphology in terms of selection. Rather, it is more likely that these difference reflect the results of isolation, inbreeding and drift.

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B. A. Sigmon

Department of Anthropology,
University of Toronto,
Canada

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A Functional Analysis of Pongid Hip and Thigh Musculature

Dissections of the hip and thigh musculature were carried out on 11 pongid specimens representing five genera (*Hylobates*, *Symphalangus*, *Pongo*, *Pan* and *Gorilla*). The functional anatomy of the hip and thigh was analyzed, and skeleto-muscular relationships were determined. Muscular function was viewed in terms of its role in locomotion. It was found that *Pongo* least well fits the anatomical pattern that occurs in the other four pongid genera. One possible explanation for this dissimilarity was suggested, and involves the orang-utan's specialized adaptation to an arboreal habitat. The anatomical data were also viewed in terms of their implications regarding the question of the evolution of erect bipedalism in hominids.

1. Introduction

The study of pongid anatomy serves two purposes. One is its direct contribution to our knowledge of pongids, and another is in providing greater insight into certain questions concerning human evolution. The relationship between pongid locomotion and anatomical regions directly affecting locomotor activity has been investigated by a number of authors. The pelvic and thigh area in particular has received considerable attention, yet the author is not aware of any comprehensive, comparative study of this anatomical region from the standpoint of correlating function and locomotion. A thorough review of the literature on the comparative anatomy of Primate hip and thigh musculature has been prepared by Uhlmann (1968). Although this is a very useful monograph, it has not dealt with comparative analyses or explanations of differences observed in Primates. Other works on this subject have often drawn conclusions based on limited anatomical data (e.g. Washburn, 1950).

Pongids are generally regarded as Man's closest living relatives. As such, studies of their morphology have been considered important stepping stones to understanding certain evolutionary developments in Man. One example of this is the investigation into the origin of erect bipedal posture and locomotion. The morphological pattern seen in the pongids is frequently alluded to as representing a close approximation of that pattern which was present in pre-hominids. Again it is the pelvic and thigh morphology that has been singled out by authors in discussions concerning the evolution of erect bipedalism.

For the above reasons the present study has been undertaken. It is an attempt to correlate anatomical function and locomotion by presenting a detailed and comparative study of the hip and thigh musculature of pongids (gibbons, orang-utans, gorillas and chimpanzees). A functional analysis of each muscle will be undertaken, differences that occur in the various taxa will be investigated, and the evolutionary significance of the findings will be briefly discussed.

2. Materials and Methods

The present study included a sample of 11 pongid cadavers in which the muscular structure of the hip and thigh was dissected and studied. The pongids that were included

in the analysis are listed below:

Species	Specimen description
<i>Hylobates</i> sp.	1 young adult male, 2 young adult females
<i>Symphalangus syndactylus</i>	1 adult male
<i>Pongo pygmaeus</i>	2 adult females
<i>Pan troglodytes</i>	1 adult male, 2 juvenile males
<i>Gorilla gorilla</i>	2 juvenile males

The general structure of each muscle, its attachments and nerve supply were documented. An interpretation of the functional anatomy was then made based on that information. The following muscles were dissected: (a) hip muscles include the iliopsoas complex (including iliacus, psoas major and psoas minor), iliотrochantericus, tensor fasciae latae, gluteus maximus, gluteus medius, gluteus minimus, piriformis, gemellus superior and inferior, obturator internus and externus and quadratus femoris; (b) the thigh muscles include sartorius, the quadriceps femoris group (rectus femoris, vastus lateralis, vastus medialis and vastus intermedius), semitendinosus, semimembranosus, biceps femoris long and short heads, adductor magnus long and short heads, adductor longus, adductor brevis, gracilis and pectineus.

The dissection technique was to reflect the skin and define the muscles as clearly and cleanly as possible. Many of the specimens had been zoo animals and as a result, contained a great deal of fatty tissue which was difficult, and in some cases, impossible to remove completely from the surrounding muscle tissue. Animals in the wild do not appear to have as much fatty tissue, and are therefore easier to analyze.

The muscles were defined by tracing the muscular or tendinous attachments completely to their point of bony or fascial origin and insertion. The nerve supply to each muscle was determined but was not traced back to its spinal origin. Muscle function was interpreted by studying the relationship between the position of the joint (fulcrum) and the attachments of the muscle in relation to that joint.

Standard human anatomical terminology is used throughout the descriptive section of the paper.* The anatomical nomenclature is that adopted by the Sixth International Congress of Anatomists in 1955, subsequently revised by the Seventh Congress in 1960 (Zuckerman, 1961; Romanes, 1964). The muscles and nerves are referred to by their anglicized name and will not include the abbreviated *M.* before or after the name of the muscle in the written description.

* An interesting problem in nonhuman dissections is that human anatomical terminology is applied to anatomical structures in non-human animals. Often the resemblances or relationships to human anatomy are very obscure, and sometimes incorrectly described as homologous structures. However, the historical circumstance and fact is that the development of a standard terminology in anatomy originated from human anatomy and this terminology has subsequently been used in anatomical works of other animals. In some ways this makes accurate description of animals closely related to Man more difficult than those distantly related because of the temptation to describe the anatomy of close relatives as mere modifications to those of Man. In actual fact, closely related animals have their own uniquely modified anatomical adaptations which should be viewed first in terms of the adaptiveness to the animals themselves.

3. Pongid Hip and Thigh Anatomy

The following discussion is a description of the hip and thigh musculature of the four pongids—the gibbon (*Hylobates*) and siamang (*Symphalangus*), the gorilla (*Gorilla*), the chimpanzee (*Pan*), and the orang-utan (*Pongo*). In the discussion these animals will often be referred to by their common rather than their generic name. Gibbon will be used when referring both to the genus *Hylobates* and *Symphalangus* except in cases where the siamang is found to be significantly different from the gibbon. The pongids are not described separately; rather variations and similarities in the muscular morphology of all four taxa are discussed together with each muscle or muscle group. This approach allows immediate inter-generic comparison.

Certain muscles that occur in pongids are not found in exactly the same form in Man. Since this may lead to terminological difficulties (because human anatomical terms are applied to nonhuman Primate anatomy), a brief summary discussing major muscular variants between hominids and pongids will precede the detailed discussion of pongid hip and thigh musculature.

Firstly, the ischiocondylar portion of adductor magnus in Man is joined to the main mass of the adductor magnus muscle. This portion is regarded as one of the hamstring muscles in Man (Woodburne, 1965), and is innervated, at least in part, by the tibial nerve which also supplies the innervation for the hamstring muscles. In pongids and some of the other nonhuman Primates, this portion of adductor magnus occurs as a separate muscle, and as such has been given various names—semimembranosus accessorius, pre-semimembranosus, ischiocondyloideus, portio n. [sic] ischiadici m. adductor magnus (Hartman & Straus, 1965), and the long head of adductor magnus (Preuschoft, 1961). In referring to the two parts of adductor magnus, the terminology used here will be according to Preuschoft who describes the muscle as adductor magnus short and long heads. In the present dissections, when the long head occurs as a separate muscle it will be described with the hamstring muscles, as its function is closely related to that of the hamstrings. Otherwise it will be included as part of the adductor group.

Secondly, gluteus maximus in Man and apes is very different in form and attachments. Blake (1967) describes gluteus maximus in nonhuman Primates as a muscular complex including three portions—tensor fasciae latae, gluteus maximus proprius and femorococcygeus. The femorococcygeus is the infero-posterior part of the gluteus maximus complex, attaching from the proximal coccygeal vertebrae to the femoral shaft. Gluteus maximus proprius is the more cranial portion arising from fascia or from a higher bony origin such as the sacrum. The human gluteus maximus appears to be most equivalent to gluteus maximus proprius and femorococcygeus. Raven (in Gregory, 1950) and Preuschoft (1961) in describing *Gorilla*, and Stern (1972) in reference to all the pongids, include both muscular portions in their definition of gluteus maximus, and this is the interpretation that will be used in the present work. Tensor fasciae latae will be described as a separate muscle, and gluteus maximus will be defined as a single muscle including gluteus maximus proprius and femorococcygeus.

Thirdly, a muscle named scansorius, which is not present as such in Man, has been found consistently in *Pongo* (Traill, 1817; Hepburn, 1892; Waterman, 1929; Boyer, 1935; Sigmon, 1969a), occasionally in the other pongids (Wilder, 1862; Champneys, 1872; Hepburn, 1892; Beddard, 1893) and sometimes in monkeys (Sato, 1965). This muscle lies on the dorso-lateral surface of the iliac blade and is innervated by the same

nerve that supplies gluteus medius and minimus. It was named scansorius by Traill (1817) because he interpreted it as a muscle capable of bringing the thigh up toward the body in a "scanning" motion.

Fourthly, a tiny muscle lying deep to iliopsoas at a position between the origin of rectus femoris and the insertion of iliopsoas, is found in some of the pongids and other nonhuman Primates. This small muscular slip has been given various names: Champneys (1872) called it iliacus internus; Barnard (1875) and Boyer (1935) described it as ilio-femoralis subrectus; Ayer (1948) called it iliacus minor; Raven (in Gregory, 1950) named it iliocapsularis; and Preuschoft (1961) and Satoh (1965) called it iliotrochantericus. Satoh (1965) also referred to it as iliocapsulo trochantericus. In Man this muscle has occasionally been found and described by the name of iliacus minor (Goss, 1962), but it does not occur regularly. In the present work this muscle will be referred to as iliotrochantericus, as it most frequently attaches to the ilium and the lesser trochanter of the femur.

The other muscles listed for inclusion in the present dissections occur in more or less equivalent positions in both Man and apes. However, this does not mean that the muscular function is the same, for the skeletal shape, especially of the ilium, is so different that a muscle capable of producing one action in pongids may produce an entirely different action in Man. Variation is also seen in specific attachments and in muscle sizes and shapes. For example, gracilis appears to have been named as such because of its gracile form in Man. In most of the pongids dissected, however, it was found to be a wide, relatively thick muscle. Yet another example is gluteus medius, so named in Man because it is medium in size in comparison to gluteus maximus and gluteus minimus. In the African pongids gluteus medius is the largest of the gluteal muscles. These and other differences will be discussed in greater detail in the succeeding pages.

(a) *Muscles of the hip*

(i) *Flexors of the hip.* The *iliopsoas complex*: Psoas major in the four pongids originates from the transverse processes and the lateral borders of the bodies and intervertebral discs of the lower half of the last thoracic vertebra, the lumbar vertebrae and the first sacral vertebra. Iliacus originates from the entire anterior surface of the iliac blade. As psoas major passes over iliacus, the fibers of both muscles unite to form the iliopsoas muscle which passes over the hip joint to insert by a stout tendon onto the medial aspect of the lesser trochanter of the femur. Psoas minor, a separate muscle from psoas major in the orangutan, chimpanzee, gorilla, siamang and one of the three gibbons, lies on the ventro-medial portion of psoas major. It rises from the lateral border of the bodies of the last thoracic and first lumbar vertebrae, and from the two corresponding intervertebral discs, and inserts by a long ribbon-like tendon onto the iliopectineal eminence of the pubis. In two of the gibbons, psoas minor is fused with psoas major, although the latter has a ribbon-like tendon which attaches onto the iliopectineal eminence as does the insertion of psoas minor in the other pongids.

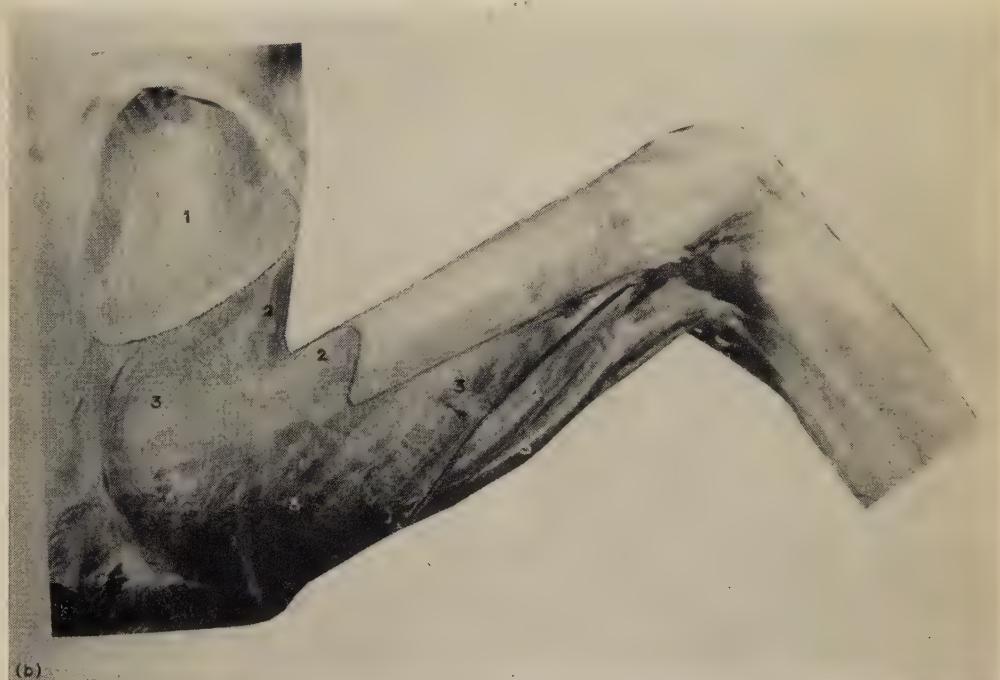
The innervation of the iliopsoas complex is from branches of the ventral rami of all the lumbar nerves to the psoas major, from the last thoracic and first lumbar nerves to psoas minor, and from branches of femoralis to iliacus. The major actions of iliopsoas are flexion of the trunk and of the thigh at the hip joint. When present, psoas minor also participates in flexion of the trunk.

Plate 1. (a) Posterior view of the hip and thigh of *Hylobates*. Ilica blade, 1; gluteus minimus, 2; tensor fasciae latae, 3; gluteus maximus, 4; long head of biceps femoris, 5; short head of biceps femoris, 6; semitendinosus, 7; gracilis, 8.



(a)

Plate 1. (b) Postero-lateral aspect of the hip and thigh of *Symphalangus*. Gluteal aponeurosis covering gluteus medius, 1; tensor fasciae latae, 2; gluteus maximus, 3; long head of biceps femoris, 4; semitendinosus, 5.



(b)

Plate 2. (a) Posterior view of the hip and thigh of *Pongo*. Gluteus maximus, 1; "ischiofemoralis," 2; long head of biceps femoris, 3; short head of biceps femoris, 4; semitendinosus, 5; gracilis, 6; semi-membranosus, 7.



Plate 2. (b) Postero-lateral aspect of the hip and thigh of *Pan*. Gluteal aponeurosis covering gluteus medius, 1; tensor fasciae latae, 2; gluteus maximus, 3; gluteal aponeurosis reflected exposing gluteus medius, 4; long head of biceps femoris, 5; short head biceps femoris, 6.



Plate 3. (a) Posterior view of the hip and thigh of *Gorilla*. Gluteal aponeurosis covering gluteus medius, 1; tensor fasciae latae, 2; gluteus maximus, 3; iliotibial band, 4; long head of biceps femoris, 5; semi-tendinosus, 6; short head of biceps femoris, 7; ischial tuberosity, 8.



Plate 3. (b) Lateral view of the thigh of *Gorilla*. Semitendinosus, 1; long head of biceps femoris, 2; short head of adductor magnus, 3; adductor brevis, 4; quadratus femoris, 5; gluteus maximus reflected to show insertion, 6; short head of biceps femoris, 7; greater trochanter of femur, 8.



(b)

Plate 4. Posterior view of the deep hip muscles of *Pan*.

(a) gluteus medius, 1; lower portion of gluteus minimus, 2; gemellus superior, 3; obturator internus, 4; gemellus inferior, 5; quadratus femoris, 6; piriformis, 7.

(b) iliac blade, 1; gluteus minimus, 2; gemellus superior, 3.

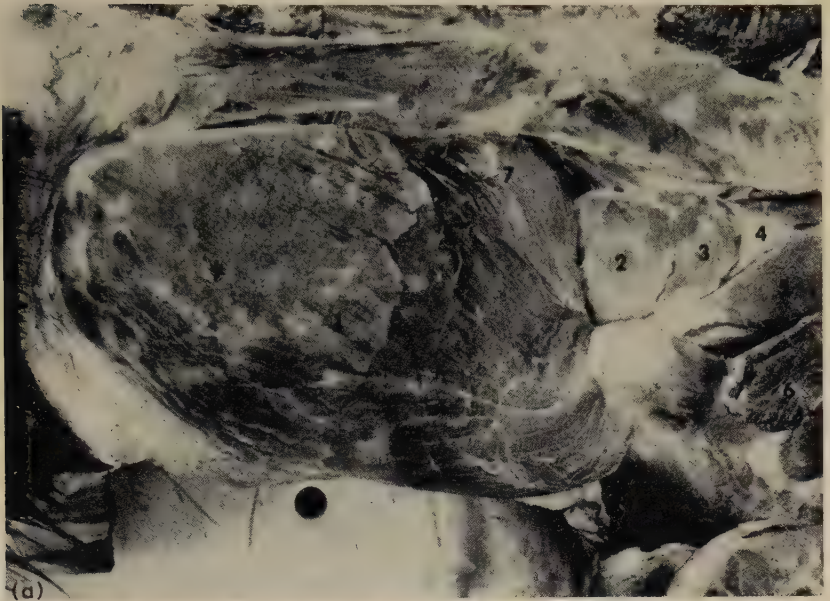


Plate 5. (a) Posterior view of the deep hip muscles of *Pongo*. Iliac blade 1; scansorius, 2; gluteus minimus proper, 3; insertion of the cranial part of gluteus maximus, 4.



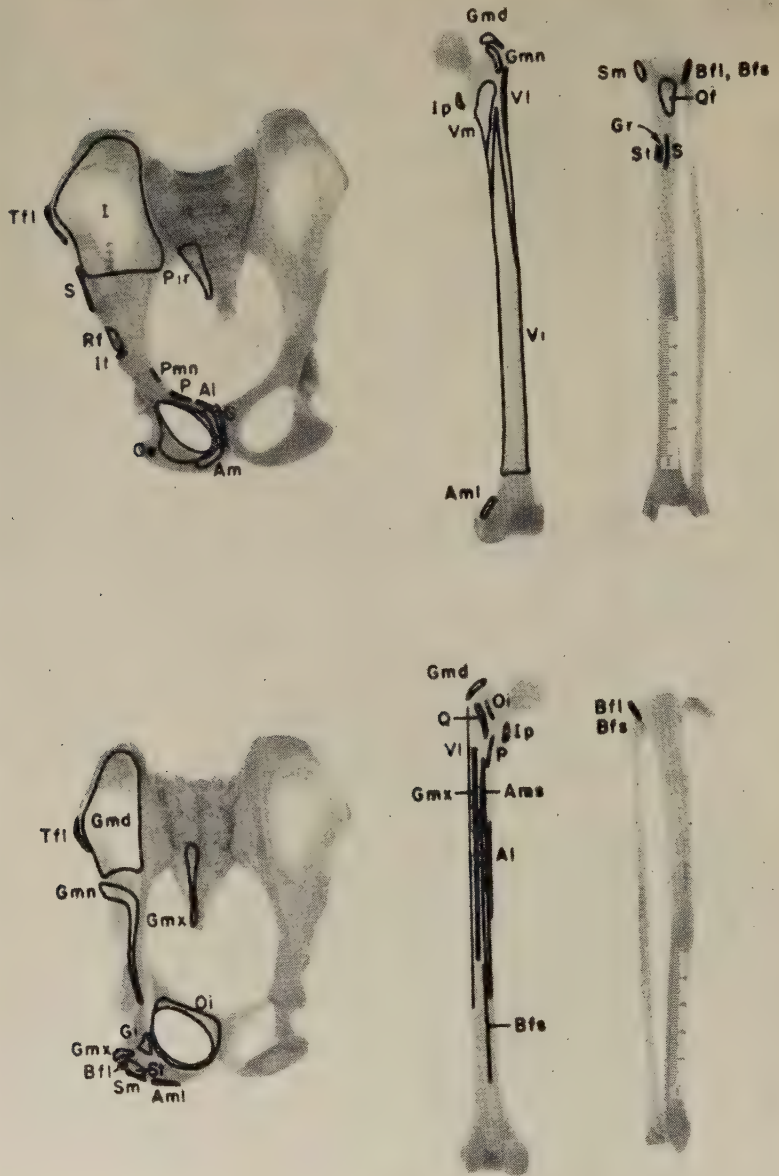
(a)

Plate 5. (b) Antero-medial view of the thigh of *Pongo*. Iliopsoas, 1; pectineus, 2; adductor longus, 3; adductor magnus, 4; insertion of the long head of adductor magnus, 4'; gracilis, 5; rectus femoris, 6; vastus medialis, 7; sartorius, 8; semimembranosus, 9; semitendinosus, 10.



(b)

Plate 6. (a) Skeletal attachments of the hip and thigh muscles of *Hylobates*. (See key to abbreviations for muscle attachments, p. 185.)
 Above: Anterior view of pelvis, femur, tibia and fibula.
 Below: Posterior view of pelvis, femur, tibia and fibula.



(a)

(See key to abbreviations for muscle attachments, p. 185.)

Above: Anterior view of pelvis, femur, tibia and fibula.

Below: Posterior view of pelvis, femur, tibia and fibula.

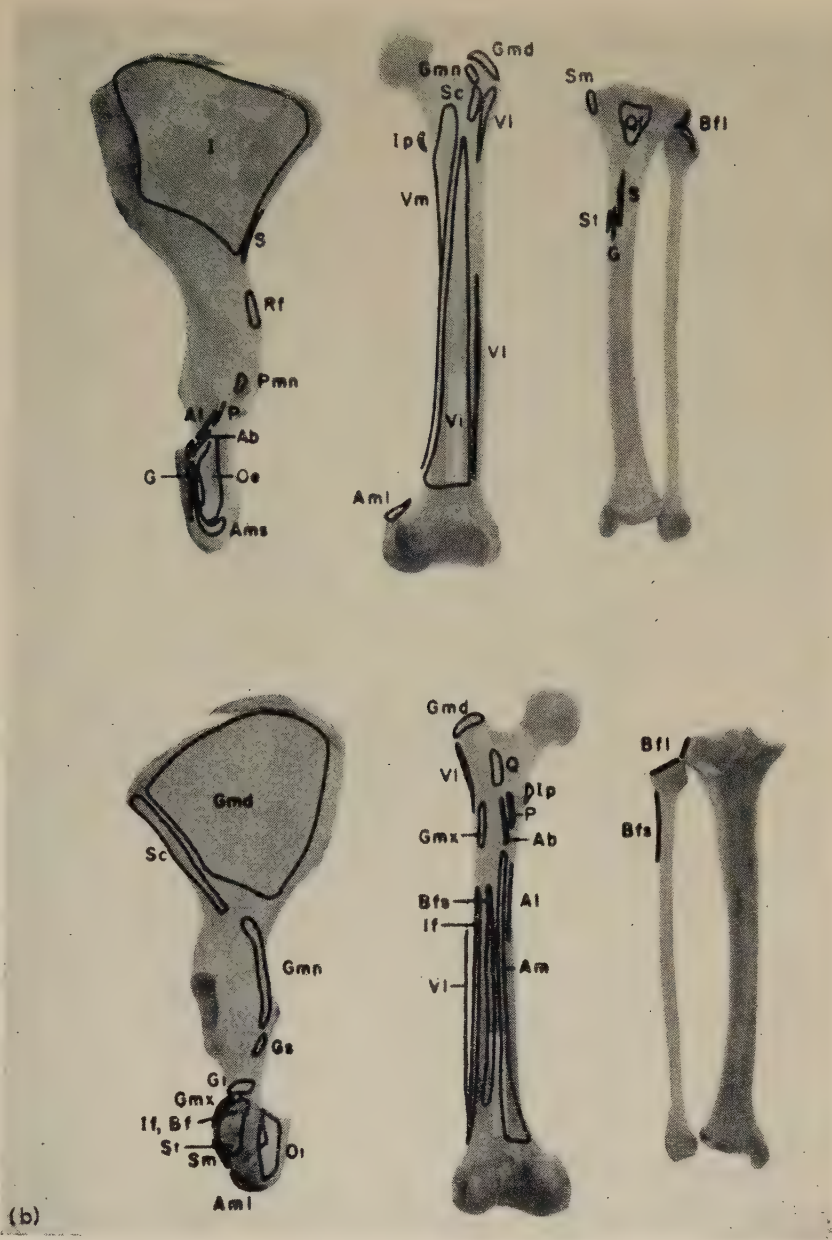
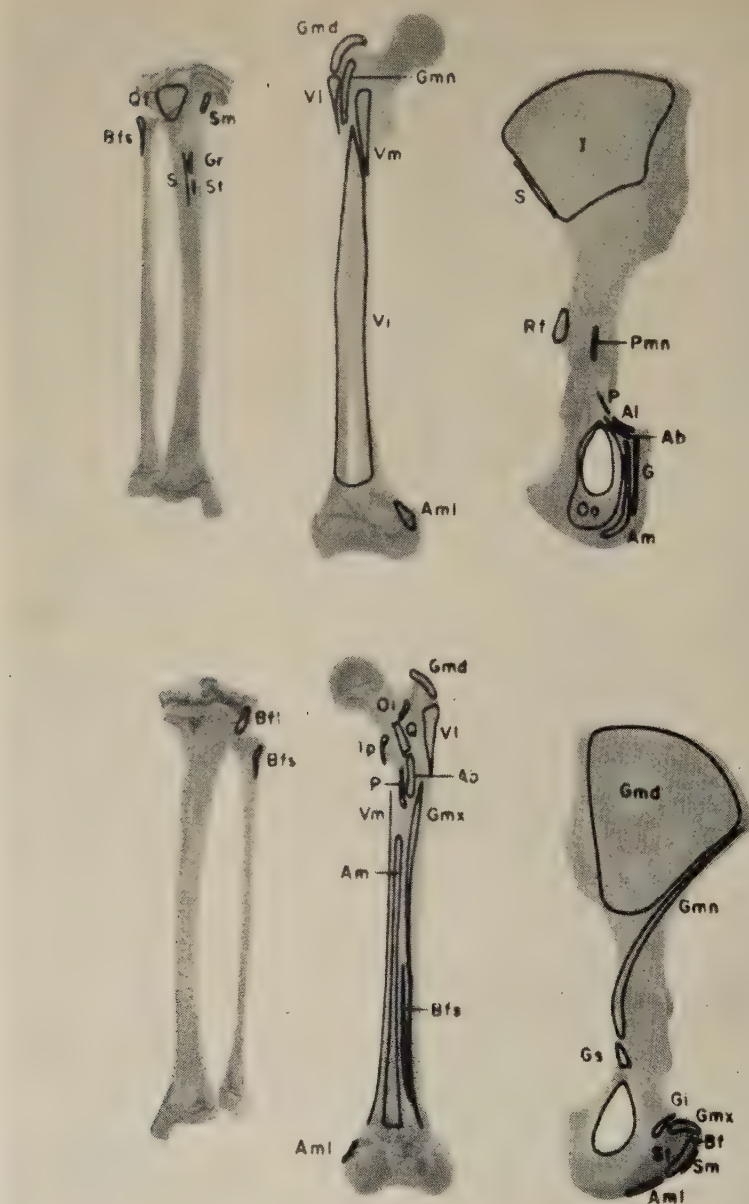
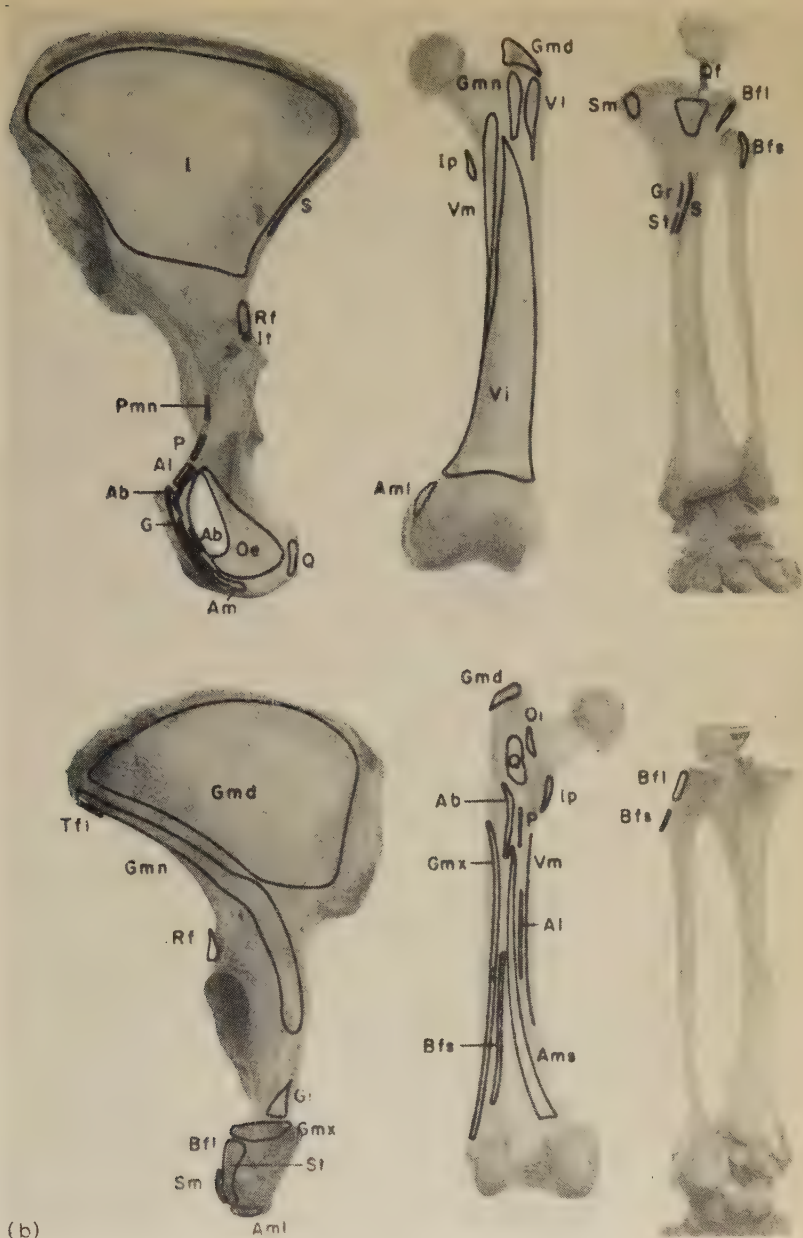


Plate 7. (a) Skeletal attachments of the hip and thigh muscles of *Pan*.
 (See key to abbreviations for muscle attachments, p. 185.)
Above: Anterior view of tibia and fibula, femur and pelvis.
Below: Posterior view of tibia and fibula, femur and pelvis.



(a)

Plate 7. (b) Skeletal attachments of the hip and thigh muscles of *Gorilla*. (See key to abbreviations for muscle attachments, p. 185.)
Above: Anterior view of pelvis, femur, tibia and fibula.
Below: Posterior view of pelvis, femur, tibia and fibula.



(b)



Iliotrochantericus has been found in the gibbon (Bischoff, 1870; Hepburn, 1892; Sonntag, 1924, and Blake, 1967), in the orang-utan (Barnard, 1875; Boyer, 1935) in the chimpanzee (Wilder, 1862; Champneys, 1872), and in the gorilla (by Raven, in Gregory, 1950; Preuschoft, 1961, and Blake, 1967). In the present dissections it was found in all of the pongids except for the siamang and one chimpanzee specimen. *Iliotrochantericus* (Figure 1) is a small slip of muscle which arises deep to, and partly from the origin of, rectus femoris and/or from the iliofemoral ligament, and inserts onto the lesser trochanter of the femur inferior to, but partly in common with, the iliopsoas muscle. The innervation in some cases could not be determined, but when it could (in the chimpanzee and gibbon), it was supplied by a branch of the femoralis nerve which in addition innervated the iliacus muscle. Satoh (1965) has also noted that *iliotrochantericus* is innervated by a branch of the femoralis nerve. This small muscle participates in flexion of the thigh, but its role is probably very minor.

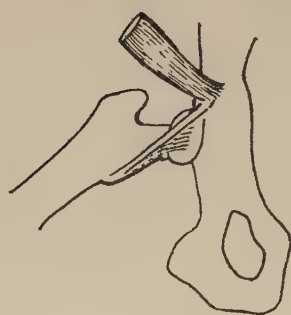
The present dissections revealed a great deal of minor variation in the attachments of this tiny muscle (see Figure 1). In two of the gibbons the muscle originates both from the tendon of origin of rectus femoris and from the iliofemoral ligament. In the gorilla and in one orang-utan the muscle arises only from the tendon of origin of rectus femoris. In the other orang-utan *iliotrochantericus* originates from the iliofemoral ligament, and in addition, a few fibers from the iliacus insert cranial to it on the iliofemoral ligament. The muscle is absent in the siamang and in one chimpanzee specimen. In the other chimpanzees the muscle is present and arises from the iliofemoral ligament; similar attachments are found for a third gibbon.

The occasional occurrence of an *iliotrochantericus* (in this instance called *iliacus minor* or *iliocapsularis*) has been observed in Man (Ayer, 1948; Goss, 1962). Bryce (1923) Goss (1962) give its attachments as the anterior inferior iliac spine and the lower part of the intertrochanteric line or the iliofemoral ligament. Bardeen (1933) describes it as a small group of muscle fibers belonging to the lateral part of iliacus and joining the tendon of origin of rectus femoris and the hip joint capsule.

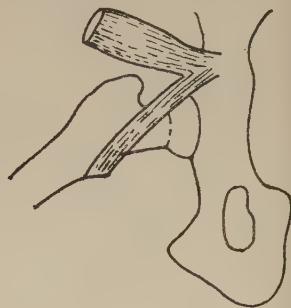
Tensor fasciae latae is present in the gibbon, chimpanzee, and gorilla. It is not found in the orang-utan. Church (1861), Hepburn (1892) and Boyer (1935) also noted its absence in *Pongo*. Perhaps in the orang-utan the antero-laterally placed scansorius has replaced it, at least in terms of function, for the scansorius also abducts and flexes the thigh and is located in a position similar to that which *tensor fasciae latae* would occupy were it present. In the former three pongids, *tensor fasciae latae* originates in the gluteal fascia. Medially it is joined to the cranial fibers of gluteus maximus; laterally it unites partly with the muscular fibers of gluteus medius and minimus, the origin extending laterally to the anterior superior iliac spine and slightly below it. The insertion is into the iliotibial tract. In the gibbon, the superior gluteal nerve innervates the more dorsal portion while a branch from the femoralis nerve supplies the antero-lateral part. Only the former innervation is present in the chimpanzee and gorilla. Raven (in Gregory, 1950) and Preuschoft (1961) also found that *tensor fasciae latae* is innervated by the superior gluteal nerve in the gorilla, but Miller (1952) listed its innervation in *Pan paniscus* as the inferior gluteal nerve. *Tensor fasciae latae* participates in flexion, abduction and medial rotation of the thigh at the hip joint. It acts with the cranial part of gluteus maximus to tense the iliotibial band, thus assisting in bracing the knee when extended.

Kaplan (1958) found that electrical stimulation of *tensor fasciae latae* in Man causes

Figure 1. The iliopsoas muscle in pongids (not drawn to scale).



(a) *Hylobates* I and II
(origin from rectus femoris
and iliofemoral ligament)



(b) *Gorilla, Pongo* I
(origin from rectus
femoris)



(c) *Pongo* II (origin from
iliofemoral ligament—a few
fibers of iliopsoas insert
onto the iliofemoral
ligament)



(d) *Pan, Hylobates* II
(origin from iliofemoral
ligament)

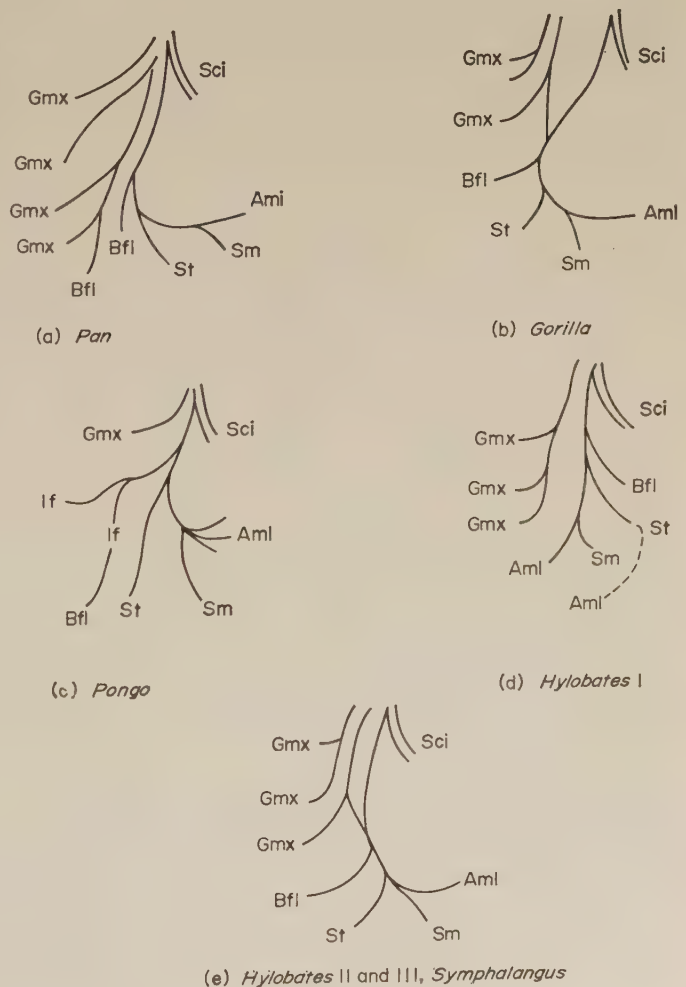
flexion and medial rotation of the thigh, but no abduction. Electromyographic studies, on the other hand, have shown that all three actions are produced by tensor fasciae latae, although its power as a rotator is weak (comment by Gardner in Kaplan, 1958; Basmajian, 1962).

(ii) *The Gluteal muscles.* *Gluteus maximus* in the gibbon, chimpanzee and gorilla (Plates 1, 2 and 3) has multiple origins and insertions: it arises from the gluteal fascia, from an aponeurosis attaching to the distal half of the sacrum and upper part of the coccyx, from the sacrotuberous ligament, and from the cranial part of the ischial tuberosity. The cranial portion of *gluteus maximus* (along with tensor fasciae latae) inserts into the iliotibial tract. The caudal portion of the muscle inserts onto the dorso-lateral region of the femoral shaft. In the gibbon the insertion extends from the gluteal tuberosity (which is at the

distal end of the greater trochanter), distally one half to two-thirds of the way down the shaft (to the origin of biceps femoris short head). The insertion in the siamang extends over the proximal four-fifths of the femoral shaft. In the chimpanzee and gorilla the insertion extends from the gluteal tuberosity all the way to the lateral epicondyle. Proximally the insertion is thick and tendinous; distally, it is thin and aponeurotic. Similar attachments from gluteus maximus in these three pongids have been recorded by Humphrey (1867), Champneys (1872), Barnard (1875), Hepburn (1892), Sonntag (1924), Raven (in Gregory, 1950), Miller (1952), Blake (1967) and Stern (1972).

The innervation is from the inferior gluteal nerve and also from a branch of the flexores femoris nerve (Figure 2). The thinner cranial part of the muscle abducts and laterally rotates the thigh; along with tensor fasciae latae it acts to tense the iliotibial band and thus to assist in bracing the knee when it is extended. The thicker distal portion is a strong extensor and also participates in adduction and lateral rotation of the thigh at the hip.

Figure 2. The innervation of gluteus maximus and the hamstring muscles. Adductor magnus longhead, Aml; adductor magnus short head, Ams; biceps femoris long head, Bfl; gluteus maximus, Gmx; ischiofemoralis, If; Sciatic nerve, Sci; Semimembranosus, Sm; and semitendinosus, St.



Gluteus maximus in the orang-utan is different from that of the other three pongids [Plate 2(a)]. It has a very fibrous texture and consistent thickness more like that found in Man. Also the muscle lies in a slightly more cranial position although the origin is similar in most respects to that of the other three pongids, that is, it arises from the gluteal fascia from strong aponeurotic fibers which attach at the medial crest of the iliac blade, from the distal half of the sacrum and coccyx and from the sacrospinous and sacrotuberous ligaments. Although it does not pass over the ischial tuberosity, there is a strong fibrous connection to the tuberosity which contains a small number of muscle fibers. It inserts by a stout tendon onto the dorso-lateral border of the proximal end of the femoral shaft and into the iliotibial band. Church (1861), Hepburn (1892), Sonntag (1924) and Boyer (1935) also found this form and these relationships for *gluteus maximus* in the orang-utan. Innervation is by the inferior gluteal nerve. The action produced by *gluteus maximus* in the orang-utan includes abduction, lateral rotation, and extension of the thigh at the hip. In addition, it tenses the iliotibial band which helps to stabilize the knee during extension of the leg.

The distal portion of *gluteus maximus* as found in the other three apes is not present as such in the orang-utan. Rather, the long head of *biceps femoris* in *Pongo* has an additional portion (which can be referred to as *ischiofemoralis*—see Preuschoft, 1961), equivalent in location and function to the distal portion of *gluteus maximus* of the other three apes. *Ischiofemoralis* [Plate 2(a)] originates in common with the long head of *biceps femoris* and attaches onto the postero-lateral border of the femoral shaft slightly distal to the insertion of *gluteus maximus*, and extends almost to the lateral epicondyle of the femur. Distally, *biceps femoris* proper becomes separate from *ischiofemoralis* and inserts below the knee joint onto the anterolateral surface of the head of the tibia and fibula. *Ischiofemoralis* is innervated by a branch of the *flexores femoris* nerve which also supplies *biceps femoris* long head. It produces thigh extension, lateral rotation and adduction as does the distal part of *gluteus maximus* in the other three apes.

Gluteus medius in the African apes [Plate 4(a)] is an extremely thick muscle that is larger by weight than *gluteus maximus* (Tables 1 and 2). In these dissections, *gluteus medius* in the gibbon was smaller and weighed less than *gluteus maximus* (Table 3). *Gluteus medius* in all of the pongids arises from the whole of the dorsum of the iliac blade and from the gluteal aponeurosis (the latter is formed by tendinous thickenings in the fascia lying between the iliac crest, the superior border of *gluteus maximus* and the iliosacral articulation). The thickness of the muscle is in part a consequence of the skeletal architecture of the pelvis. Superficially the muscle lies in an even line with the dorsal edge of the sacrum, whereas at its attachment on the ilium it is convex, corresponding to the concave dorsal surface of the iliac blade. Generally, the muscular fibers run in a cranio-caudal direction, and the muscle has a very fleshy appearance. Caudomedially the distal fibers of *piriformis* unite with those of *gluteus medius*. These two muscles end abruptly in a short, stout tendon that inserts onto the antero-lateral border of the greater trochanter.

Gluteus medius is always innervated by the superior gluteal nerve. The muscle is an important thigh extensor and also acts in abduction and medial rotation of the thigh at the hip joint.

Gluteus minimus in the gorilla and chimpanzee [Plate 4(b)] arises from an extensive region on the dorso-lateral border of the ilium and from a portion of the ischium. The origin is from the anterior superior iliac spine and curves around fan-like, extending

Table 1

Muscle weights as a percentage of total weight of the hip joint muscles

	<i>Hylobates</i>	<i>Gorilla</i>	<i>Pan</i>	Man	Author
Gluteus maximus		13.3%	11.7%	18.3% 11.1	Haughton (1873)* Voss (1956) Preuschoft (1961) Blake (1967)
	10.4	10.8 11.7			
Gluteus medius		14.0	14.6	12.3 4.5	Haughton* Voss Preuschoft Blake
	8.1†	11.2 15.5†			
Gluteus minimus		1.8	4.2	3.5 1.5	Haughton* Voss Preuschoft Blake
	2.5	2.6 3.4			

Muscle weights are an indicator of size and functional importance of a muscle. The figures show that in Man and the gibbon the muscle weights are largest for gluteus maximus, smaller for gluteus medius and least for gluteus minimus (as the names were probably meant to imply). Muscle weights for the African apes indicate that gluteus medius is somewhat heavier than gluteus maximus.

* Haughton expressed the weights as a percentage of total hip musculature, but did not include the quadriceps femoris muscles in his calculations.

† Blake included piriformis in his figure for gluteus medius, thus the percentage is slightly higher than it should be.

Table 2

The muscle weights of gluteus maximus as a percentage of gluteus medius

	<i>Hylobates</i>	<i>Gorilla</i>	<i>Pan</i>	<i>Pongo</i>	Man
Haughton (1873)		0.95	0.80		1.48
Tappen (1955)	0.40*				
Voss (1956)					2.47
Preuschoft (1961)		0.96			
Blake (1967)	1.27 (0.54*)	0.75			
Sigmon (1969b)	1.44			0.87†	

* Blake's calculation of 0.54 includes only gluteus maximus proprius. Notice how similar it is to the ratio from Tappen's data. This indicates that probably only gluteus maximus proprius was included in Tappen's study. Tappen (1968) has been unable to verify this.

† This figure includes only gluteus maximus proper, not ischiofemoralis. The inclusion of ischiofemoralis as a part of gluteus maximus would give a figure greater than 1, making it the largest of the gluteal muscles in *Pongo*.

caudally to the ischial spine. This fan-shaped muscle narrows into a wide, flat tendon which inserts onto the anterior surface of the greater trochanter of the femur, medial to the origin of vastus lateralis.

In the gibbon [Plate 1(a)] gluteus minimus arises more caudally on the dorso-lateral surface of the iliac blade (about midway between the anterior superior iliac spine and the upper rim of the acetabulum). Its origin, as in the African apes, curves caudally,

Table 3

Gluteal muscle weights for *Hylobates*

	Tappen (1955)		Blake (1967) Weight (g)	Sigmon (1969b)
	Left	Right		
Gluteus maximus	4.2*	+3.7	10.3 (4.4*) (5.9†)	3.1
Gluteus medius	10.0	10.0	8.1	2.1
Gluteus minimus	3.2	2.7	2.5	

* Gluteus maximus proprius only.

† Femorococcygeus only.

extending to the ischial spine. Again the muscle is fan-shaped, ending in a wide, flat tendon which inserts onto the anterior surface of the greater trochanter of the femur. Gluteus minimus in the siamang lies in the same position and has the equivalent attachments as are found in the gibbon, except that the muscle is divisible into two parts at its insertion.

The form of gluteus minimus in the orang-utan [Plate 5(a)] is different from that in the other three pongids. Whereas in the African apes gluteus minimus is one undivided muscle extending from the anterior superior iliac spine to the ischial spine, in the orang-utan there are two distinctly separable muscles lying in this position. The muscle lying in the more lateral position arises from the dorso-lateral border of the iliac blade from the anterior superior iliac spine caudal to about midway between that spine and the upper rim of the acetabulum. The second muscle, which lies in a more medial position, arises from the ilium at a position just distal to the medial portion of the iliac blade and the sacroiliac articulation, that is, along the dorsal area of the greater sciatic notch, and extends to the ischial spine. The latter muscle which is somewhat fan-shaped narrows to a tendinous insertion onto the anterior surface of the greater trochanter of the femur. The more laterally located muscle, triangular in shape, inserts by a stout tendon onto the greater trochanter just distal to the insertion of the aforementioned muscle.

Whether gluteus minimus is one undivided muscle as in the chimpanzee, gorilla and gibbon (in the siamang it is only partly divisible), or two separable muscles as in the orang-utan, the innervation is always by the superior gluteal nerve and the major action is abduction of the thigh. In addition the lateral portion or muscle, as the case may be, produces flexion and medial rotation, and the medial portion, or muscle, can laterally rotate and possibly extend the thigh.

Examination of the literature reveals that the pattern and arrangement of the deep gluteal musculature of the orang-utan is similar in all respects to that found in the present dissections. The first person to apply a name other than gluteus minimus to one of these two muscles in the orang-utan was Traill (1817). The medially placed muscle was considered the gluteus minimus proper, but in reference to the laterally located muscle Traill says:

"The most remarkable muscle about the top of the thigh, has not been noticed by Tyson, Camper, Cuvier, or the older anatomists. It is a flat triangular muscle, arising from the whole anterior edge of the ilium to within half an inch of the acetabulum, and is inserted just below the forepart of the great trochanter, between the head of the cruralis and vastus externus, a little below the origin of the former. It is thin and fleshy through its whole extent, except where it is inserted by a very short-flattened tendon. At its upper part, it is united by cellular

substance to the iliacus internus. The action of this muscle, which appears to be peculiar to this animal, is to draw the thigh up toward the body; and it seems especially to be intended to assist in climbing. On this account we propose to name it the *scandens*, or *Musculus Scansorius*; and we are disposed to regard it as one of the principal peculiarities of *Simia Satyrus*." (Traill, 1817: 28-29).

Since then others have noted the presence of *scansorius* (as well as *gluteus minimus* proper) in the orang-utan (Hepburn, 1892; Waterman, 1929; Boyer, 1935). Also from the description that Barnard (1875) gives, it appears that he found two muscles in the orang-utan equivalent to *scansorius* and *gluteus minimus*, but he called them, respectively, *gluteus minimus*—which appeared to him to be greatly misplaced—and *piriformis*.

There is a great deal of variation in the descriptions of dissections of the deep gluteal musculature of the chimpanzee, and to a lesser degree of the gorilla. Wilder (1863) and Hepburn (1892) described the presence of a distinct *scansorius* in the chimpanzee. Champneys (1872) and Beddard (1893) noted in the chimpanzee that *scansorius* could be separated from *gluteus minimus* only with some difficulty. Blake (1967) described *scansorius* in the gibbon and gorilla. Others failed to find *scansorius* either in the chimpanzee (Humphrey, 1867; Sutton, 1884) or in the gibbon and gorilla (Hepburn, 1892). Preuschoft (1961) described *gluteus minimus* in the gorilla as being partly divided at origin but with the fibers fusing distally (see his drawings, p. 450). He called the lateral portion the "pars scansorica" of the *gluteus minimus*, and the caudo-medial portion the *gluteus minimus* proper. A detailed discussion of *scansorius* in pongids can be found in Sigmon (1969a).

The present dissections reveal that *gluteus minimus* in the orang-utan is divided into two distinctly separable muscles—a laterally placed *scansorius*, and a more caudo-medially located *gluteus minimus* proper. The two muscles occur in the same position as the continuous undivided *gluteus minimus* of the other three apes, and the innervation and actions are similar. The only other noticeable differences are that in the orang-utan *scansorius* appears to be a slightly thicker muscle that is located on the iliac blade somewhat more antero-laterally than the lateral portion of *gluteus minimus* of the other three pongids. Because of the similarities in the deep gluteal musculature of all four apes in innervation, location, and function it would appear that *scansorius* in the orang-utan is equivalent and probably homologous to the cranio-lateral portion of *gluteus minimus*, especially as seen in the African pongids (although somewhat reduced in the gibbon). Traill named this separate muscle *scansorius* because he considered its importance to be in climbing, allowing the thigh a "scanning" range of movement. The actions of flexion, abduction and medial rotation of the thigh at the hip joint would substantiate this functional interpretation. Its flexing action appears to be more powerfully developed than the comparable portion of *gluteus minimus* in the other pongids. This may be partly in compensation for the absence of *tensor fasciae latae* in the orang-utan, but which in the other pongids is present and participates in flexion of the thigh.

(iii) *The lateral rotator-abductor group* [Plate 4(a)]. *Piriformis* arises from the ventro-lateral surface of the distal half of the sacrum. It passes dorsally through the greater sciatic notch after which its fibers unite with those of *gluteus medius*. Both muscles insert together onto the antero-medial border of the greater trochanter of the femur, the *piriformis* portion lying slightly more medial. Actions produced by *piriformis* are lateral rotation and abduction at the hip.

Gemellus superior is not present in all of the pongids. In the animals dissected it was found only in the chimpanzees and in one orang-utan. When it is present, it arises from the dorso-lateral surface of the ascending ramus of the ischium between the ischial spine and the ischial tuberosity. It inserts into the trochanteric fossa by a tendon common to both gemelli (superior and inferior) and to obturator internus. The actions produced by this muscle include abduction and lateral rotation of the thigh.

The occasional absence of the superior gemellus muscle has also been noted in Man. Terry (1942) described its absence both unilaterally or bilaterally in 8.6% of American White and in 14.5% of American-born Negroes. Other authors (Wood, 1867; Loth, 1931) have given slightly lower figures for its absence.

Gemellus inferior is present in all of the pongids, arising from the inferior ramus of the ischium just cranial to the ischial tuberosity, and inserting into the trochanteric fossa by a tendon common to gemellus superior and obturator internus. Its actions include abduction and lateral rotation of the thigh.

Obturator internus and *externus* are similar in all four pongids. *Obturator internus* arises from the inner surfaces of the pubis and ischium around the obturator foramen, and from the obturator membrane. Its insertion into the trochanteric fossa is by a tendon common also to the gemelli. *Obturator externus* takes origin externally from the border of the obturator foramen including a large portion of the inferior pubic ramus, and from the obturator membrane. It inserts by a short, thick tendon into the trochanteric fossa caudal to the insertion of the gemelli and obturator internus. Abduction and lateral rotation are produced by both obturator muscles.

Quadratus femoris is a small but thick, fleshy muscle. It arises inferiorly from the antero-lateral surface of the ischial tuberosity, and inserts on the intertrochanteric crest of the femur cranial to the insertion of pectineus. The muscle is an abductor and lateral rotator of the thigh at the hip joint.

Piriformis, the gemellus muscles, quadratus femoris and obturator internus are innervated by sacral nerves via the sacral plexus. *Obturator externus* receives its nerve supply from a branch of the obturator nerve.

(b) *Muscles of the thigh*

(i) *The anterior thigh muscles* [Plate 5(b)]. *Sartorius*, as in Man, is flat and strap-like. It originates by short tendinous fibers from the lateral border of the iliac blade just below the anterior superior iliac spine, and inserts by a wide tendon on the upper third of the antero-medial surface of the tibia. The innervation is from the femoralis nerve, and the muscle acts in thigh and knee flexion; in addition, it medially rotates the leg, and laterally rotates and abducts the thigh.

The *quadriceps femoris* muscles which include rectus femoris, vastus lateralis, vastus medialis and vastus intermedius are similar in the four apes. They form a large muscle mass covering the entire lateral and anterior surface of the thigh in addition to much of the medial and part of the dorso-lateral regions of the thigh. Although the origin of each muscle is separate, all four have a common insertion onto the tuberosity of the tibia via the ligamentum patellae, which forms a strong tendinous capsule over the anterior, antero-medial, and antero-lateral surfaces of the knee joint. *Rectus femoris* arises from a well-defined tubercle—which corresponds to the anterior inferior iliac spine in Man—on the lateral border of the ilium just above the acetabulum. There was a second but smaller tendinous head of origin lying inferior to the first head in one orang-utan but

all the other pongids, including a second orang-utan, had only one head of origin. *Vastus lateralis* arises by a stout tendon from the lateral surface of the greater trochanter of the femur; a small, narrow head arises from the iliofemoral ligament (this origin is separated from the larger head by the insertion of gluteus minimus and scansorius when the latter is present); the third origin is from the distal two-thirds of the lateral surface of the femoral shaft. The gibbon lacks the second, narrow head of origin, and the attachment from the greater trochanter is continuous with that onto the femoral shaft so that the origin of *vastus lateralis* in the gibbon is a single attachment extending from the greater trochanter of the femur to the distal third of the femoral shaft. *Vastus medialis* arises from the iliofemoral ligament and the entire postero-medial surface of the femoral shaft, the origin being continuous from the ligament to the distal end of the shaft. The origin in the gibbon extends only onto the proximal two-thirds of the femoral shaft. *Vastus intermedius* originates from almost the whole of the anterior surface of the femoral shaft. It lies somewhat inferiorly between the *vastus medialis* and *lateralis*, and its cranial extension is rather narrow. The quadriceps femoris muscles are innervated by branches of the femoralis nerve. The group as a whole are knee extensors; in addition, the rectus femoris which is the only two-joint muscle of the group, assists in thigh flexion.

(ii) The *hamstrings* (Plates 1, 2 and 3) which include *semitendinosus*, *semimembranosus*, *biceps femoris*—and in this paper will also include the long head of *adductor magnus*—are generally similar in the four apes except with regard to *biceps femoris* and the long head of *adductor magnus*. *Biceps femoris* varies among the pongids with respect to the extent of its attachments and the presence or absence of the short head. *Adductor magnus* long head can occur either as a separate muscle or as a muscular portion joined with *adductor magnus* short head.

Hamstring origins: all of the hamstring muscles (except the short head of *biceps femoris* which is not classified as a hamstring muscle but which is sometimes united with the long head of *biceps femoris*) arise from the ischial tuberosity. *Semitendinosus* and *biceps femoris* long head arise together by a short, stout tendon from the infero-lateral surface of the ischial tuberosity; *semimembranosus* arises by a flat, ribbon-like tendon at a position more inferior and lateral than the origin of the latter two muscles; and *adductor magnus* long head arises by a short, stout tendon from the most infero-medial border of the origins of the above three muscles, and extends around to the anterior end of the tuberosity, next to the inferior pubic ramus. *Biceps femoris* short head in the African pongids arises by muscular fibers from the dorso-lateral surface of the distal third of the femoral shaft; in the gibbon the origin is similar but does not extend as far distally; and in the orang-utan the origin extends further cranially to include the distal two-thirds of the femoral shaft.

Hamstring insertions: *semitendinosus* inserts by a long narrow tendon onto the antero-medial surface of the tibia about one-third of the way down on the shaft, just distal to the insertion of *gracilis* in the African pongids and medial to *gracilis* in the orang-utan and gibbon. *Biceps femoris* long head is completely separate from the short head with respect to origin and insertion in the two gorillas, the two orang-utans and in two of the chimpanzees. In the other chimpanzee and in the gibbons and siamang the arrangement of the two heads of *biceps femoris* is similar to that found in Man, that is, the short head joins the long head and they insert together by a wide tendon onto the lateral prominence of the tibia. In the African apes in which the two heads are separate muscles, the long head inserts into the lower fibers of the iliotibial tract and onto the antero-lateral border

of the head of the tibia; the short head inserts just distal to the long head, into the crural fascia of the leg and onto the lateral head of the fibula.

The orang-utan represents a different arrangement for biceps femoris in that the long head is composed of two distinct muscular portions which arise jointly from the ischial tuberosity, but which are separable distally. The one-jointed portion (which was referred to as ischiofemoralis in the section describing gluteus maximus) inserts on the dorso-lateral surface of the femoral shaft from just below the insertion of gluteus maximus and extends almost to the lateral epicondyle of the femur. It was stated previously that the ischiofemoralis portion of biceps femoris in the orang-utan is comparable in location and function to the caudal portion of gluteus maximus of the other three pongids. The other portion should be considered the biceps femoris long head proper, and is similar in insertion to that of the other pongids; specifically it inserts below the knee joint on the head of the fibula, the lateral condyle of the tibia, into the distal part of the iliotibial tract, and into the crural fascia of the leg. The short head of biceps femoris inserts into the crural fascia and onto the lateral border of the proximal end of the fibula.

Semimembranosus in all of the pongids inserts by a short, narrow tendon onto the medial eminence of the head of the tibia. The *adductor magnus long head* is a distinct muscle separate from the adductor magnus short head in the African pongids and in two of the gibbons. In these animals the muscle inserts by a stout tendon onto the medial epicondyle of the femur. In the orang-utans, the siamang and in one of the gibbons, the proximal portions for the long and short heads are united and there is no separation of the two at their origin; however, distally the short and long heads become separate and the long head inserts by a short, stout tendon on or near the medial epicondyle of the femur, as found in the other pongids.

The flexores femoris nerve (Figure 2) innervates the hamstrings (including adductor magnus long head but excluding biceps femoris short head). According to Hartman & Straus who edited a detailed anatomical study of *Macaca mulatta* (1965), the flexores femoris nerve arises from L4, L5 and L6, or from L6, L7 and S1, and runs beside the tibialis nerve to the upper part of the thigh where it gives off branches to semitendinosus, biceps femoris long head and semimembranosus. The relationships in the pongids dissected in the present study were similar. Although the tibialis nerve is present, it does not provide innervation for the hamstrings. In Man there is no flexores femoris nerve; rather, the hamstrings are innervated by branches of the tibialis nerve. In all of the pongids biceps femoris short head is innervated by branches of the common peroneal nerve.

All of the hamstrings (including adductor magnus long head but not biceps femoris short head) function as thigh extensors. Semitendinosus, biceps femoris long and short heads and semimembranosus are also important knee flexors. In addition to these actions, semitendinosus and semimembranosus rotate the thigh medially, biceps femoris long head rotates it laterally and adductor magnus long head adducts and laterally rotates the thigh.

(iii) The *adductor muscles* [Plate 5(b)] are parts of one muscle mass, and their attachments are often united or lie very close together at origin or insertion. *Adductor longus* arises by a short, flat tendon from the anterior surface of the superior ramus of the pubis between pectineus and gracilis. It inserts onto the medial border of the femoral shaft beside and anterior to the proximal half of the insertion of adductor magnus short head. *Adductor brevis* is present in all of the pongids except the gibbon in which the muscle appears to be a portion of the short head of adductor magnus. In the other pongids,

adductor brevis has two origins: one is from the superior ramus of the pubis at a position inferior to adductor longus; the other arises from the pubic symphysis between adductor magnus short head and obturator externus, and is partly joined with the former. Both parts join to share a common insertion onto the dorsal surface of the femur distal to the lesser trochanter and lateral to the insertion of pectineus. An *adductor minimus* muscle was not found in any of the pongids. The *adductor magnus long head* which arises from the ischial tuberosity has been described with the hamstrings; it is a separate muscle in all the pongids except the orang-utans, the siamang and one gibbon. In all cases its insertion is onto the medial epicondyle of the femur or slightly proximal to the epicondyle as in the siamang. *Adductor magnus short head* arises by a stout tendon from the pubis just lateral to the symphysis and inferior to gracilis. It extends the length of the inferior pubic ramus, and inserts onto the postero-medial surface of the femur. In the African apes and the orang-utan the insertion covers the distal two-thirds of the shaft to about the intercondylar region, but in the gibbon the insertion is onto the middle third of the femoral shaft. In the orang-utans, the siamang and one gibbon, where the adductor magnus long and short heads are united, there is a slight separation between the fibers of insertion of the two heads, the long head inserting onto or near the medial epicondyle of the femur, and the short head inserting on the distal one-half to two-thirds of the dorso-medial surface of the femur.

The obturator nerve innervates the adductors longus, brevis and magnus short head. Flexores femoris nerve supplies the innervation for adductor magnus long head, and in the orang-utans, the siamang and one gibbon in which the two heads of adductor magnus are united, the short head receives innervation from both flexores femoris and the obturator nerve. Adductor longus, brevis and magnus short head act as flexors, medial rotators and adductors of the thigh. Adductor magnus short and long heads are powerful adductors. As mentioned earlier, adductor magnus long head also extends and laterally rotates the thigh.

Gracilis is a wide, flat muscle, larger than that found in Man. It arises lateral to the pubic symphysis and inserts on the proximal third of the antero-medial surface of the shaft of the tibia, medial to the insertion of sartorius. The obturator nerve supplies its innervation. Adduction, flexion and medial rotation are actions produced by gracilis.

Pectineus arises by a short tendon from the most cranial portion of the superior pubic ramus, usually cranial to the origin of adductor longus, and inserts onto the dorsal surface of the femoral shaft somewhat distal and lateral to the lesser trochanter. The femoralis nerve supplies its innervation. In one of the orang-utans, the origin was partly inferior to adductor longus although the muscle still extended more cranially than the longus; in addition, the muscle fibers of pectineus were partly joined with those of adductor longus. The branch of the obturator nerve which supplied the adductor longus also provided the innervation for the pectineus in this case. The muscular arrangement in the second orang-utan was similar to that found for the other pongids. The function of pectineus includes adduction, flexion and medial rotation of the thigh at the hip joint.

4. Muscles and Movement

(a) *Comparative summary of pongid hip and thigh musculature*

The hip and thigh in *Pan*, *Gorilla* and *Pongo* can be generally characterized as having fleshy, usually thick, robust musculature. By comparison, the muscles of *Hylobates* and

Symphalangus are proportionately longer and more slender. In terms of more specific muscular morphology, *Pan* and *Gorilla* have been shown to have virtually no anatomical differences in hip and thigh musculature, and except for a few minor variations, the gibbon is very similar to the African apes. *Pongo*, however, has a very different muscular arrangement particularly with respect to gluteus maximus, gluteus minimus, biceps femoris and tensor fasciae latae.

Looking at the first muscle group that was described, the flexors of the hip, variation in the iliopsoas complex occurs only in the degree of separation of psoas minor. The iliopsoas complex shows minor variations, and in addition it is occasionally absent. Tensor fasciae latae is absent in the orang-utan, and it differs slightly in form between the gibbon and the African apes. In the gibbon it occurs as a lateral continuation of the cranial part of gluteus maximus, wrapping around gluteus medius along the lateral border of the iliac blade to which it attaches. Tensor fasciae latae occurs as a more distinguishable muscle in the African pongids where proximally it is fused only with the cranial fibers of gluteus maximus. In all cases it inserts into the iliotibial tract.

Gluteus maximus in the gibbon and African apes shows little variation in attachments or form. In all three the cranial portion is thin, and the caudal part extending between the ischial tuberosity and the femoral shaft is thick and powerfully developed. Gluteus maximus in the orang-utan is different in form and in certain of its attachments. Firstly, the cranial part of the muscle in *Pongo* is thicker, more fleshy, and covers a more extensive area of the hip than does the cranial part of gluteus maximus in the other pongids. Secondly, the distal ischio-femoral portion is not joined to the cranial part of gluteus maximus. It is a separate muscle, and is often referred to as the ischiofemoralis muscle, yet it lies in roughly the same position as the distal part of gluteus maximus in the other three pongids. Furthermore, the action that it is capable of producing is the same as its counterpart in the other pongids.

Gluteus medius shows no differences in attachment or overall form in the pongids, but the arrangement of gluteus minimus is variable. In the African pongids gluteus minimus is a single muscle covering an extensive area of the lateral iliac surface and the upper ischium. The area of attachment is smaller in the gibbon where the muscle originates further caudally on the ilium. Gluteus minimus in the orang-utan is divided into two parts which cover the same general area as that of the African apes: gluteus minimus proper is located on the caudal part of the ilium and the cranial part of the ischium, and a *pars scansorius* lies on the lateral surface of the iliac blade. Except for the fact that gluteus minimus in the orang-utan is divided into two separate muscles, and that the lateral scansorius part has a more anterior placement, it is essentially similar in location and function to that of the African pongids.

Little variability occurs in the lateral rotator-abductor group. The absence of gemellus superior is noted for the gorilla, gibbon and one orang-utan specimen. In a second orang-utan and in the chimpanzees it is present.

The anterior thigh muscles show some variability in the origins of rectus femoris and vastus lateralis. Usually there is only one head of origin for rectus femoris; however, in one of the orang-utans there is a second more inferior tendinous head. Vastus lateralis, except in the gibbon has a second small muscular head of origin arising from the ilio-femoral ligament. In the gibbon vastus lateralis has one continuous attachment onto the femoral shaft from the greater trochanter to the distal end of the shaft. The other apes show a separation between the cranial and caudal origins, the upper-middle part of the muscle belly not being attached to the femur.

The hamstring muscles (including adductor magnus long head) differ among the pongids chiefly with respect to biceps femoris and adductor magnus long head. In the gorilla, orang-utan and two chimpanzees, the short and long heads of biceps femoris occur as separate unjoined muscles. The long head inserts onto the lateral head of the tibia and into the iliotibial tract, and the short head inserts distal to the long head into the crural fascia and onto the lateral head of the fibula. The short and long heads of biceps femoris in the gibbon and in one chimpanzee specimen are united, and insert together by a wide tendon onto the lateral head of the tibia. An ischiofemoralis muscular portion, joined proximally to the long head of biceps femoris in the orang-utan has already been discussed with gluteus maximus. Adductor magnus long head is a separate muscle in the African apes and in two of the gibbons. In the orang-utans, the siamang and one gibbon the long and short heads of adductor magnus are united proximally, but the muscles become separate distally and insert separately. In all cases the long head of adductor magnus inserts onto or near the medial epicondyle of the femur.

The major variation that occurs in the adductor muscles is discussed in the hamstring section, and concerns the degree of separation of the long and short heads of adductor magnus. In one orang-utan the muscular fibers of pectineus are joined with those of adductor longus, but in every other case these two muscles are separate. In most respects the adductor muscular mass is similar in all the pongids. The following muscles are always present in roughly the same form and position: adductors longus, brevis and magnus short and long heads. The latter two heads are always distinct parts even when they share the same origin. Gracilis in the African pongids and the orang-utans is always a wide, flat muscle; in the gibbon it is long and slender as are most of the thigh muscles.

A summary of the skeleto-muscular relationships can be seen in Plates 6 and 7.

(b) *Pongo as different from the other pongids*

As the preceding discussion has shown, chimpanzees, gorillas and gibbons have basically the same pattern of hip and thigh musculature. The orang-utan deviates somewhat from the pattern seen in the other three pongid taxa. A possible explanation for this variation may be related to the differences in habitat and to the locomotion that is most efficient and effective in a given environment.

Basically all of the pongids are adapted for arboreal quadrupedalism. Yet as such this is a generalization that tells us very little about their range of locomotion or their more specific movements. A question of particular relevance, therefore, is whether or not the orang-utan uses different movements that could provide us with clues for interpreting why it has the muscular pattern that we find for it.

Table 4 shows us that there are no specific locomotor habits practiced by the orang-utan that do not also occur in the other pongids. The only difference that can be seen from the table is that orang-utans are not terrestrial in their natural environment nor are they adept brachiators (Carpenter, 1938; Schaller, 1961). They inhabit peat swamp rain forests where the peat substratum may be covered with several feet of water, making terrestrial movement impractical or impossible (Schaller, 1961, 1965). A more recent study (Horr, 1972a) ascribes occasional terrestrial activity to orang-utans; even so, Horr also concludes that orang-utans are predominantly arboreal (1972b).

Terrestrial quadrupedalism and occasional bipedalism are important elements of the locomotor repertoire in the other pongids. The suggestion from these observations is that orang-utans may have adapted certain specializations for climbing about in trees,

Table 4 **Modes of locomotion in pongids**

	Gibbon	Orang-utan	Chimpanzee	Gorilla
Nissen (1931)			Quadrupedalism— arboreal and terrestrial, downward jumping and leaping, bipedalism rare	
Carpenter (1938) Carpenter (1940)	Predominantly brachiation, some arboreal bipedalism, climbing, jumping	Arboreal quadrupedalism		
Kortlandt (1962)			Predominantly terrestrial quadrupedalism, some arboreal quadrupedalism and bipedalism	Predominantly terrestrial quadrupedalism, some tree climbing, bipedalism infrequent
Schaller (1963, 1965)				
Goodall (1965)			Quadrupedalism— arboreal and terrestrial, some brachiation and bipedalism	
Reynolds (1965); Reynolds & Reynolds (1965)			Quadrupedalism— arboreal and terrestrial, some climbing and brachiation	
Schaller (1965)	Predominantly brachiation, some arboreal bipedalism	Arboreal quadrupedalism, some brachiation	Quadrupedalism— arboreal and terrestrial	
Horr (1972b)		Predominantly arboreal		

especially since their locomotion is limited almost entirely to tree movement. Climbing is an important means of locomotion in the other pongids as well, but alternative types of locomotion are either predominant or can occur frequently, for example brachiation in the gibbon, terrestrial quadrupedalism in gorilla, and terrestrial as well as arboreal quadrupedalism in chimpanzees. Thus, a specialized climbing adaptation may not have been as selectively critical to these pongids as it appears to be for *Pongo*.

In reviewing the ways in which *Pongo* differs anatomically from the other pongids, we can see how the differences might be related to the orang-utan's predominant form of locomotion, arboreal quadrupedalism which includes a large amount of climbing.

Firstly, gluteus maximus in *Pongo* has a fibrous, coarsely textured structure which grossly resembles that of Man. It is different from that of the other pongids in the sense that it lies a little more cranially, is a thicker muscle, and is separate from the distal portion, or the ischiofemoralis muscle, that lies between the ischial tuberosity and the femoral shaft. The particular structure and position of gluteus maximus proper in the orang-utan makes it a more powerful thigh abductor than is the cranial part of gluteus maximus in the other pongids, and in addition allows abduction to be performed independently of actions such as extension and lateral rotation produced by ischiofemoralis. This slight difference in availability of additional muscle power for abduction that could be utilized independently of ischiofemoralis might be very important to an animal that relies heavily on tree climbing.

A second peculiarity of *Pongo* is the division of gluteus minimus into two muscles including the caudo-medially located gluteus minimus proper and the antero-laterally positioned *pars scansorius*. In the other pongids, gluteus minimus is usually a continuous undivided muscle covering almost as extensive an area in the African apes as that covered by the two muscles in *Pongo*. In addition, the functions are similar: *pars scansorius* in *Pongo* produces flexion, abduction and medial rotation of the thigh, as does the antero-lateral part of gluteus minimus in the African apes; gluteus minimus proper can abduct, medially rotate, possibly extend the thigh, as can the caudo-medial part of gluteus minimus of the African apes. However, an important difference in the muscular arrangements is in the amount of power capable of being produced by *scansorius* in comparison to that produced by the lateral portion of the gluteus minimus muscle. *Scansorius* is thicker and is located more antero-laterally, thus its actions in flexion, abduction and medial rotation would tend to be more powerful.

The division of gluteus minimus into a *scansorius* and a gluteus minimus proper could also be advantageous to an arboreal climber like *Pongo* because it would free one muscle—*scansorius*—to participate in a scanning movement of the thigh in climbing as Traill (1817) suggested when he named the muscle. That is, a division of gluteus minimus could allow the anterolateral part (*scansorius*) to act in flexion, abduction and medial rotation from a different vantage point and independently from that of the caudo-medial part (gluteus minimus proper) which also acts in medial rotation and abduction. This would mean that the two muscles could respond at slightly different times within a given movement, adding to it a larger range of muscular activity, possibly an important advantage to thigh activity used in climbing.

Finally, the long and short heads of biceps femoris in *Pongo* occur as two separate muscles, thus following the same pattern as that found for the gluteal muscles. Although this is not a unique arrangement, for the two heads are also separate muscles in *Gorilla* and sometimes in *Pan*, it is worth noting because of the tendency in *Pongo* for muscles

to be separate rather than single fused units. The short head of biceps femoris acts over the knee joint in knee flexion. Biceps femoris long head crosses the hip and the knee joint and acts in extension and lateral rotation of the thigh, and flexion at the knee. The division of the two muscular parts could again be adaptive in the sense of increasing the range of independent muscular activity useful in climbing movements.

In summary, *Pongo* differs considerably from the other pongids with regard to attachments, structure and relationships—but not basic function—of gluteus maximus, gluteus minimus and to some extent biceps femoris. The absence of tensor fasciae latae is also a unique feature. Of the three gluteal muscles, gluteus maximus and gluteus minimus in *Pongo* are different from the other pongids primarily in the sense that they both consist of two separate muscular portions (gluteus maximus = gluteus maximus proper and ischiofemoralis, and gluteus minimus = gluteus minimus proper and scansorius). Biceps femoris is divided into two separate muscles, biceps femoris long head and biceps femoris short head. The long head is different from the other pongids because of the presence of ischiofemoralis.

Abduction of the thigh at the hip joint is obviously an important action in climbing, and we have seen how gluteus maximus and gluteus minimus are specialized to produce effective abductor function. In addition, in an animal like the orang-utan that requires a great deal of freedom in movement for climbing about in trees, the separation of functional components of all these muscles would seem to be adaptive in the sense of providing greater independent action of various parts of the muscle as it acts at the hip or the knee joint. Thus, it would appear that certain aspects of the muscular anatomy and subsequent locomotion of the orang-utan may be related to specialized adaptations that have enabled it to function most effectively as an arboreal, quadrupedal climber.

On the other hand, the anatomical pattern common to the other pongids, and differing from that of *Pongo*, apparently meets all their locomotor needs, be it brachiation, terrestrial or arboreal quadrupedalism, and terrestrial or arboreal bipedalism. Thus one is tempted to regard theirs as the more generalized hip and thigh anatomical pattern, particularly as it is shared by three different taxa whose evolutionary separation probably occurred as long ago as the Miocene. Paleontologically, one cannot say which specific pongid form occurred earlier and thus might be ancestral to the others. The fossil record distinguishes only a generalized ape-like form, *Aegyptopithecus*, in the Upper Oligocene. By Miocene times the four pongid taxa that we recognize today were more or less differentiated. The morphological gap between the latter and the generalized Oligocene ape has yet to be filled.

Thus, the most likely explanation for the occurrence of these anatomical differences and similarities is that the more general ancestral pattern has been retained in *Pan*, *Gorilla* and *Hylobates*, whereas *Pongo* has undergone certain specialized adaptations due to its more restricted habitat and subsequent locomotor habits. It is unlikely that parallel evolution could explain the presence of such a similar anatomical pattern in three different taxa.

(c) *Pongid musculature and hominid posture*

A second result of this study is that it shows that gluteus maximus in the apes is not primarily an abductor of the thigh as was suggested by Washburn (1950) and has frequently been described as such in subsequent papers and in introductory physical

anthropology textbooks (e.g. Breitingner, 1962; Eimerl DeVore, 1965; Campbell, 1966; Buettner-Janusch, 1966; Snyder, 1967; Hulse, 1971). Not all authors, however, have interpreted the muscle as such (e.g. Blake, 1967; Stern, 1972); this includes earlier ones from the nineteenth century (e.g. Wilder, 1862; Bischoff, 1870, 1880; Primrose, 1898, 1899).

One of the major actions of gluteus maximus in pongids, as well as in Man, is extension of the thigh at the hip joint. Regarding the muscle as primarily a thigh extensor makes a very big difference in the interpretation of evolutionary changes that occurred in the development of erect bipedalism in hominids. A detailed discussion of these changes can be found in Robinson (1968; 1972) and Robinson, Freedman & Sigmon (1972) and therefore will only be briefly treated here.

A condensed summary of the above works shows that, with respect to understanding changes that came about in the evolution of erect bipedalism in hominids, the significant differences in hip and thigh musculature of pongids and Man lie not in the actions that the individual muscles can perform (Table 5 shows the overall similarity in gluteal

Table 5 Functions of the gluteal musculature in pongids and Man

	Pongid	Man
Gluteus maximus	Extension Lateral rotation Abduction (cranial part) Abduction (lower part)	Extension Lateral rotation Abduction (cranial part) Abduction (lower part)
Gluteus medius	Abduction Extension Medial rotation	Abduction Extension (lower fibers) Medial rotation Lateral rotation (lower fibers) Flexion (anterior fibers)
Gluteus minimus	Abduction Possibly some extension (lower fibers) Medial rotation Lateral rotation (lower part) Flexion (cranio-lateral part)	Abduction Extension (lower fibers) Medial rotation Lateral rotation (lower fibers) Flexion (cranio-lateral part)

All functions listed are of the thigh at the hip joint.

muscular actions in pongids and hominids), but (1) in a shift from a pongid thigh extensor arrangement that is power-oriented to a hominid one that is speed-oriented, an observation first noted by Robinson (1968), and (2) in the development of a more effective lateral balance control during erect bipedal walking (Robinson *et al.*, 1972).

Thigh extension in pongids is accomplished predominantly by gluteus maximus, gluteus medius and the hamstring muscles. (Napier, 1967 has noted that gluteus medius and gluteus minimus in pongids act as thigh extensors; however, he does not include gluteus maximus as an extensor.) In hominids thigh extension is due to gluteus maximus and the hamstring muscles; gluteus medius, and also gluteus minimus in hominids are predominantly abductors of the thigh, aiding in lateral balance control during erect bipedal walking. (Stern, 1972 has suggested that gluteus maximus plays a major role in lateral balance control. This will be discussed shortly.)

Two major anatomical differences in pongids and hominids therefore are firstly in the muscular *effect* that can be produced by the hamstrings and gluteus maximus, rather than in the action alone as these muscles are extensors in both taxa, and secondly in the shift in the major action of gluteus medius which in pongids is extension and in hominids is abduction.

In understanding how a muscle in two different taxa can produce the same basic action yet have a very different effective result in locomotion, Robinson *et al.* (1972) have referred to an article by Smith & Savage (1956) who discuss the roles of lever and moment arms of muscles and the effect of differences in general proportion of the skeletal elements to which muscles attach. In applying these ideas to the pelvic girdle and lower limb skeleton of apes and Man, the authors pointed out a notable difference in the two taxa. This was first described by Robinson in 1968 and subsequently in more detail (Robinson, 1972). He demonstrated the importance of the difference in apes and Man in relative lengths of ischial tuberosity, femur and overall length of the lower limb. Without going into great detail, the notable differences found were that the ischial tuberosity (the effective moment arm) is longer in apes than in Man, whereas the femur and the total lower limb (lever arms) are shorter in apes than in Man. As these are the major areas of attachment of the hamstrings and of gluteus maximus in apes, the resulting effect of the muscular action produced is different in the two taxa. In physical terms a long moment arm and short lever arm results in a powerful force; a short moment arm and long lever arms produces a force that is relatively faster but weaker and which has a wider range of movement.

The thigh extensor mechanism therefore in quadrupedal apes is adapted for power; that in Man is adapted for speed and range of movement. These differences would appear to highly correlated with the locomotion predominantly practiced by the respective taxa: power in pongids for use in climbing, jumping and general quadrupedal movements; and speed and wide range of movement in Man for upright bipedalism.

The second major difference in pongids and Man is gluteus medius, and to a lesser extent gluteus minimus. Lateral balance control at the hip joint is necessary in bipedal walking and is effectively produced in Man by gluteus medius and gluteus minimus which act to support the hip on the contralateral side of the supported limb. The lateral balance control mechanism is undeveloped in pongids where gluteus medius is positioned so as to act most effectively as an important and powerful thigh extensor. This shift in the major effect that gluteus medius can produce in pongids and hominids was a primary factor contributing to the development of upright bipedalism in hominids. Stern (1972) has suggested that the iliac attachment and the cranial migration as well as the cranial thickening of gluteus maximus in hominids has been an important adaptation related to the development of lateral balance control in erect bipedal walking and in slow running. There is, however, little evidence to support that gluteus maximus in Man acts in abduction which is the major action in lateral balance control. Some recent electromyographic studies (Jonsson & Steen, 1963; Karlsson & Jonsson, 1965) have shown that gluteus maximus can produce abduction under conditions where heavy muscular effort is required. But whether or not gluteus maximus is important in, or even contributes to, lateral balance control during upright walking or running is far from having been demonstrated.

In summary little difference can be detected when comparing the actions of individual muscles of pongids and hominids. One must go beyond this interpretation of anatomical differences to analyze the resulting functional effect that a muscle or a group

of muscles can produce. It is only by looking at this overall functional effect that one can hope to make sense from the relationship between anatomy and locomotion.

5. Summary

Many authors have either referred to or have discussed the hip and thigh morphology of pongids with reference to a particular point they wished to make concerning pongid and/or hominid evolution. These discussions have sometimes been based on inaccurate or inadequate data. The present paper is an attempt to present the anatomical picture of the hip and thigh of each member of the family Pongidae. This has been done by describing the attachments, innervation and function of each hip and thigh muscle. Certain of the findings, particularly regarding the gluteal muscles, are incongruous with some of the things which have been written about them (e.g. Washburn, 1950). It is hoped that the descriptive data presented in this paper may be useful to authors who find occasion to refer to pongid hip and thigh morphology in their discussions.

A comparative analysis of the five pongid genera studied showed that *Pongo* differs from the other pongids in certain anatomical aspects. From what we know of pongid locomotion, *Pongo* is the most dependent on an arboreal, climbing existence. It was suggested that the orang-utan's muscular structure is due to specialized adaptations related to a greater efficiency for climbing in trees.

The anatomical results were also viewed in terms of their implications regarding the evolution of hominid erect bipedalism. In the hip and thigh, the most significant differences between pongids and hominids are to be found in the gluteal and hamstring muscles. It is not the action of the muscles that are different; the differences lie in the effect that the muscles can produce as a function of their skeleto-muscular relationships (Robinson, 1968; 1972). The pongid thigh extensor muscles are adapted for the production of power whereas the hominid extensors are specialized for speed and wide range of movement. Secondly, the two deeper gluteal muscles, gluteus medius and gluteus minimus, in hominids are effective in producing lateral balance control necessary during walking upright. These two muscles in pongids, particularly gluteus medius, are ineffective in this capacity; the major function of gluteus medius in pongids is in thigh extension.

In conclusion, the study of the soft anatomy of the hip and thigh in pongids yields information not only about their morphology, but provides us with clues regarding the evolution of the hominoid lineage.

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Key to Abbreviations for Muscle Attachments (Plates 6 and 7)

Ab	Adductor brevis	Oe	Obturator externus
Al	Adductor longus	Oi	Obturator internus
Aml	Adductor magnus long head	P	Pectineus
Ams	Adductor magnus short head	Pir	Piriformis
Bfl	Biceps femoris long head	Pmj	Psoas major
Bfs	Biceps femoris short head	Pmn	Psoas minor
G	Gracilis	Q	Quadratus femoris
Gi	Gemellus inferior	Qf	Quadriceps femoris
Gmd	Gluteus medius	Rf	Rectus femoris
Gmn	Gluteus minimus	S	Sartorius
Gp	Gluteus minimus proprius	Sc	Scansorius
Gmx	Gluteus maximus	Sm	Semimembranosus
Gs	Gemellus superior	St	Semitendinosus
I	Iliacus	Tfl	Tensor fasciae latae
If	Ischiofemoralis	Vi	Vastus intermedius
Ip	Iliopsoas	VI	Vastus lateralis
It	Iliotrochantericus	Vm	Vastus medialis

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Following the recommendation of the participants of the Primate Chromosome Conference held in Detroit, August 1973, the *Journal of Human Evolution* will devote a certain number of pages in each issue to the publication of banded karyotypes of different Primates.

Cytogeneticists interested in publishing karyotypes should submit to the Editor at least three copies of a banded metaphase with their proposed karyotype arrangement of the chromosomes.

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R. I. M. Dunbar
Patsy Dunbar

Department of Psychology,
University of Bristol, England

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On Hybridization Between *Theropithecus gelada* and *Papio anubis* in the Wild

Evidence is presented which suggests that *Theropithecus gelada* and *Papio anubis* may interbreed in the wild. The behavioural and ecological circumstances which give rise to this are discussed. The implications of these observations to the taxonomic status of these genera are assessed.

1. Introduction

Hybrids between different genera of Primates have been bred in captivity with some success (see reviews by Chiarelli, 1961 and Buettner-Janusch, 1966). In the wild, hybrids are less common and have been reported only between species of the same genus (*Papio anubis* $\times$ *P. hamadryas*, Kummer, 1968, Nagel, 1971; *P. anubis* $\times$ *P. cynocephalus*, Maples, 1972; *Macaca nemestrina* $\times$ *M. irus*, Bernstein, 1966; *Cercopithecus mitis* $\times$ *C. ascanius*, Aldrich-Blake, 1968; *C. mona* $\times$ *C. pogonias*, *C. erythrotis* $\times$ *C. cephus*, Struhsaker, 1970). In most cases, the existence of these hybrid swarms have been attributed to the disruption of the normal niche separation between the species concerned as a result of destruction of the habitat by Man.

The present study reports 3 cases of possible hybridization in the wild between two species of different genera, *Theropithecus gelada* and *Papio anubis*. Hybrids between *Theropithecus* and *Papio hamadryas* have been successfully bred at the Sukhumi Research Station in Russia (Markarian *et al.*, 1972).*

2. Results

The geographic distribution of *Papio anubis* in Ethiopia overlaps that of *T. gelada* on the Amhara plateau, to which the latter species is confined (Figure 1). In general, however, there is marked ecological separation between the two species even in areas where they co-exist (Crook & Aldrich-Blake, 1968). The gelada are restricted to the steep sides of the deep gorges which dissect the plateau, while the anubis are found only where gallery forest occurs along river beds or lake margins and in isolated patches of relict *Juniperus/Olea* and other forest. This habitat preference is further strengthened by marked contrasts in diet, gelada being almost totally graminivorous whereas anubis baboons are predominantly fruit and seed eaters (Crook & Aldrich-Blake, 1968). Thus, areas in which the two species are actually sympatric are likely to be few.

* Since this paper was completed, Professor B. A. Lapin (*in litt.*) has informed me that *Theropithecus* $\times$ *Papio anubis* hybrids have also been bred successfully at the Sukhumi Research Station. As with the *Theropithecus* $\times$ *P. hamadryas* hybrids, these animals are fertile, and the *Theropithecus* phenotype dominates in all cases.

Figure 1. Distribution of baboons in Ethiopia, showing locations where each species is known to occur. ●, *Papio anubis*; +, *P. hamadryas*; ▲, *Theropithecus gelada*; 1, Wolkefit Pass; 2, Blue Nile gorge; 3, Debra Libanos; 4, Bole Valley; 5, Upper Cassam Valley.



Four areas were located on the plateau where the two species co-exist (see Figure 1): these were Debra Libanos (see also Crook & Aldrich-Blake, 1968), the Blue Nile gorge in the vicinity of the Shiffatak bridge, the Bole Valley, and the Wolkefit Pass on the Simien escarpment. All these areas were visited on a number of occasions, but in only one (the Bole Valley) were the two species ever observed together in mixed species parties. [However, Holt (1972) reports observing a mixed species party on the Wolkefit Pass on another occasion.]

Among the gelada groups in the Bole Valley, one contained three individuals (a sub-adult female and two juvenile males) which differed from normal gelada. These individuals were all identical in appearance. They resembled gelada in physical structure and possessed the callosities and areas of bare skin on the chest typical of that species. The fur, however, was short and apparently coarse, and bluish-grey in colour, except on the tail where it was pale yellow. This was in marked contrast to the long, silky brown

fur of gelada, and resembled more closely the shorter grey fur of *P. anubis*. In the case of the female, the muzzle appeared to be slightly longer and straighter than is typical of gelada.

Examination of slides of the Sukhumi *T. gelada* $\times$ *P. hamadryas* hybrids (kindly supplied to us by Dr H-J. Kühn) shows that these hybrids also resemble gelada in physical appearance, except for a greyish tinge to the fur. In certain other features (e.g. muzzle shape) they are intermediate between the two species. Unfortunately we were unable to get close enough to the Bole Valley animals or to obtain good enough photographs for a detailed comparison to be made, but the two groups of animals are similar in showing a closer superficial resemblance to gelada.

While it may yet be possible that the three Bole Valley animals are not hybrids, but simply pathological freaks, the possibility that hybrids could occur in the wild is strengthened by the fact that inter-specific copulations were observed on a number of occasions.

The three individuals were well integrated members of their social unit. The subadult female was nulliparous, and showed no signs of reproductive activity during the five month study period. This may be considered unusual in females of her age: in most cases they would already have given birth, or be pregnant. At the very least, they would be showing signs of estrous. This individual gave no indication of doing so, and we were inclined to conclude that she was probably infertile. However, the hybrids bred between gelada and *P. hamadryas* at Sukhumi are fertile (Markarian *et al.*, 1972).

During a total of 209 hr of observation on one or other of the species in the Bole Valley, they formed mixed species parties for a total of 21 hr 45 min, or 10.4% of the time. These parties might last from a matter of 10 min to as long as two or three days of intermittent contact. During this time, 23 interactions were observed between members of the two species: seven were agonistic, three were friendly (involving play and grooming among juveniles) and the remaining 13 were sexually oriented. Of the sexual interactions, two involved adult anubis females in estrous and 11 involved juvenile anubis females in estrous. In all cases except one, the recipient was a sub-adult or juvenile male gelada, the exception being when an adult anubis female approached, peered at and then presented rear to an adult gelada male. In all cases except one, the anubis female initiated the interaction, generally by approaching gelada males and presenting rear. In five instances, the male mounted the female, of which two did not involve intromission. In at least two cases, ejaculation did not occur.

During none of the observations made on mixed species parties were any of the gelada females in estrous. Consequently we cannot determine whether this pattern of behavior was reciprocated by the gelada females, or whether it was typical only of anubis females.

Juvenile females of many Primate species are of less sexual interest to their males than adults, and neither gelada nor anubis adult males mount juvenile females in estrous nearly as often as they do adults. It seems likely, therefore, that the young females are more willing to seek sexual interaction elsewhere. In the present case, there were, in addition to the juvenile males of their own troops, large numbers of young gelada males available. Since groups of the two species quite frequently came into contact (the anubis groups concerned spent over 20% of their time in mixed species parties), the opportunity for inter-specific copulations are plentiful. Although it is likely that the first few estrous cycles in most species are infertile (cf. Rowell, 1963, in the case of *Macaca mulatta*), it may nonetheless sometimes happen that such a female is fertilized and hybrids result.

3. Discussion

While only detailed serological examination could determine the genetic affinities of the animals observed at Bole, the evidence for sexual activity between the two species at least demonstrates that hybrids could occur. The low frequency of such individuals in the population (three out of a total of 243 gelada and 140 anubis in the valley) is no doubt accounted for by the low probability of fertilizations among juveniles and the casual nature of the interactions between the two species. The marked ecological separation between them clearly accounts for the fact that such individuals were not observed elsewhere.

In contrast, hybrids between *P. anubis* and *P. hamadryas* are common in the Awash valley (Nagel, 1971). It seems likely that these have resulted from the active invasion of anubis troops by young hamadryas males in search of females with which to form harems (Kummer, Goetz & Angst, 1970). This situation does not seem to occur between gelada and anubis.

Only two areas are known where gelada and hamadryas are sympatric (see Figure 1): in the upper Cassam valley (Kummer, 1968) and in the Simien Mountains (Crook & Aldrich-Blake, 1968). (It is, however, likely that the two species meet at a chain of points along the eastern escarpment line where the Amhara plateau gives way to the lowlands of the Danakil desert.) In both of these areas the hamadryas are apparently only seasonal visitors. During the course of an 11 month field study in the Simien, we encountered hamadryas bands on five occasions between May and October, but not at all between November and March. Even when parties of the two species do meet, they rarely remain together for any length of time since the hamadryas' greater rate of movement and longer day-range length (12–15 km as against 1–2 km for gelada) invariably lead to the rapid dispersal of such parties. Although the two species did spend the night together on two occasions, the hamadryas rapidly outdistanced the gelada the following morning. The only interactions observed between individuals of these two species to date have all been agonistic (one case by Kummer, 1968; four by Crook & Aldrich-Blake, 1968; and two by ourselves). Thus it seems that the even more marked ecological separation between gelada and hamadryas serves to reduce the likelihood of hybridization to negligible values.

The occurrence of hybrids between gelada and anubis at Bole seems to be unusual, and may perhaps result from human interference in the ecosystem through intensive agriculture. Typically, the anubis prefer the flat open ground of the plateau top. This area, however, is under heavy agricultural use, and the local farmers are generally successful in keeping the anubis down on the gorge side, with the result that they come into more frequent contact with the gelada than would otherwise probably be the case.

The gelada occupy a somewhat uncertain position taxonomically (Hill, 1970; Jolly, 1972). The present observations tend to add weight to Buettner-Janusch's (1966) contention that the species should be included in the genus *Papio* on biochemical grounds. Sarich (1970), for instance, was unable to find any differences between the albumins of *Papio* and *Theropithecus*. On these grounds, the retention of *P. hamadryas* as a distinct species from the *P. cynocephalus* supersp. may be unwarranted since the differences between them are considerably less than those which separate off *Theropithecus* from either of them. However, Nagel (1971) suggests that *P. hamadryas* should be retained as a full species on the grounds that it shows marked morphological and behavioural differences from the cynocephalus baboons, some of which at least are genetically determined.

Hybridization data alone may not be of great significance at such taxonomic levels, since as Chiarelli (1968) pointed out, these species plus *Macaca* and *Cercocebus* can all interbreed.

The facts that *Theropithecus* is phylogenetically much older than hamadryas (Jolly, 1972) and shows even greater morphological and behavioural differences from *Papio* would argue in favour of its retention as a distinct genus. The genetical affinities between the various species can perhaps be best reflected in the division of the group into a number of tribes and retaining the present generic and specific designations, as suggested by Jolly (1966, 1972) and Hill (1970).

4. Summary

Three possible cases of hybridization between *Theropithecus gelada* and *Papio anubis* in the wild are described. The circumstances under which inter-generic copulations were observed are analysed, and it is concluded that fertilizations probably occur only rarely in the wild since mostly juvenile and subadult animals are involved. Human interference in the ecosystem has resulted in a breakdown of the natural ecological separation between the two species. It is concluded that hybrids between *T. gelada* and *P. hamadryas* are unlikely to occur in the wild due to the more marked ecological separation between them.

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Warren G. Kinzey

*Department of Anthropology,
City College of the City University
of New York, Convent Avenue at
138th Street, N.Y., New York
10031, U.S.A.*

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Ceboid Models for the Evolution of Hominoid Dentition*

Platyrrhine and catarrhine Primates have independently evolved such features of the teeth and jaws as U-shaped dental arches, reduced cingula on molars and premolars, and modifications for small tough-object feeding. The presence of specialization for tough-object feeding in arboreal cebids such as *Cebus apella* and *Callicebus* indicates that hominids may have acquired such a specialization in an arboreal habitat before becoming terrestrial.

1. Introduction

Since the 18th century naturalists have recognized the attainment of a "monkey" grade of Primate organization in both the Neotropics and the Old World tropics. The morphological similarities between the New World (platyrrhine) and the Old World (catarrhine) Primates are well known (Hill, 1957). Although platyrrhine and catarrhine Primates have been isolated from one another for millions of years the exact time and place of their paleogeographic separation remains uncertain. The traditional point of view (Simpson, 1945; Stirton, 1951; Napier, 1970; Buettner-Janusch, 1971) is that the platyrrhines were derived from a North American prosimian ancestor by an island-hopping invasion early in the Tertiary. Gregory (1922) suggested the Notharctinae as the ancestral stock and others (Simons, 1961, 1969; Gazin, 1958) have suggested the Omomyinae. The presence of an early Tertiary holarctic land bridge between North America and Europe (McKenna, 1972a) has lent support to the latter view by establishing a dispersal route for the (omomyine) common ancestor of the Platyrrhini and Catarrhini.

A difficulty with the traditional point of view, however, is that recent biochemical evidence (Goodman, 1967; Goodman *et al.*, 1971; Sarich, 1970) indicates a much closer similarity between platyrrhine and catarrhine Primates than between either group and prosimians; whereas, the final separation of the Eurasian and North American land masses at least 47 million years ago (Pitman & Talwani, 1972) places the most recent possible common prosimian ancestor for the entire anthropoid stock in Early Eocene (Sparnacian) times (McKenna, 1972b). Another possible dispersal route for platyrrhines has become more tenable with recent evidence for a Cretaceous South Atlantic land bridge (Keast, 1972). Continental drift between South America and Africa began in the Mesozoic and during the early Tertiary the two continents were closer together than they are today. Rafting of early Primates across the narrow South Atlantic from Africa to South America was possible since South Atlantic ocean currents during the Eocene and Oligocene were apparently from East to West (Frakes & Kemp, 1972). Finally, the sudden appearance in the South American Early Oligocene (Deseadan) of both cavio-morph rodents and platyrrhine Primates increases the likelihood of an early Tertiary origin from West Africa for both groups (Hershkovitz, 1972; Hoffstetter, 1972). A Late

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Eocene or Early Oligocene divergence of platyrrhines and catarrhines also admits the possibility that their common ancestor had already attained an anthropoid grade of organization. Irrespective of grade attained by the common ancestor, rafting across the South Atlantic allows more recent common ancestry for all Anthroidea than does dispersal across a North Atlantic land bridge.

The possibility of a more recent (than Early Eocene) common ancestor for New World and Old World Primates emphasizes the importance of examining the former as an aid to the understanding of evolution of the latter. The study of platyrrhine-catarrhine parallelisms has already proved useful in interpreting Primate locomotor adaptations (Erikson, 1963; Stern, 1971). In this paper I shall be concerned with the nature of parallelisms in the jaws and teeth of platyrrhine and catarrhine Primates, specifically with similarities between Ceboidea and Hominoidea, and with implications of the study of cebid dentition for a model of early hominid dental evolution.

2. Evidence of Parallel Evolution

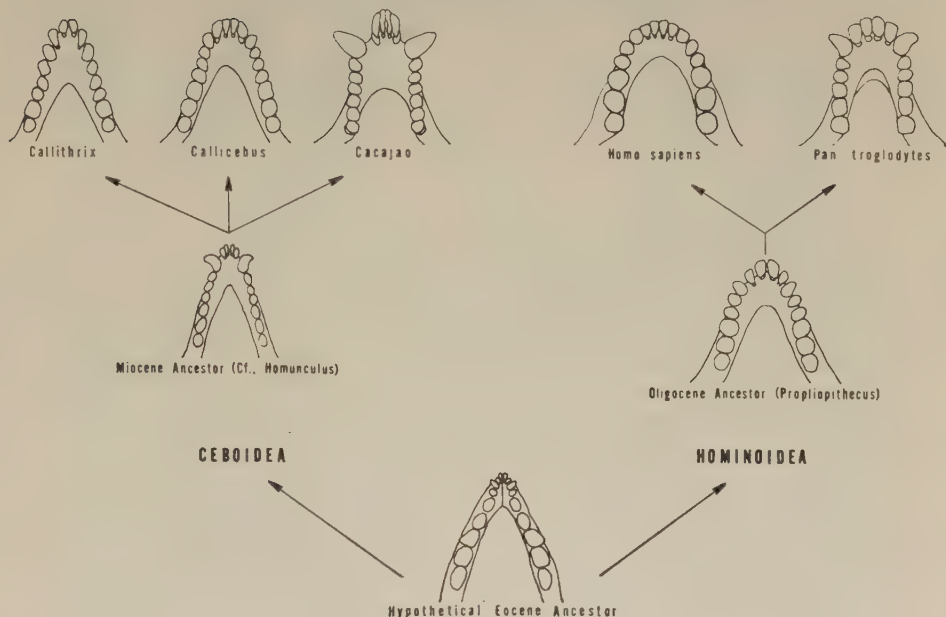
The general similarity of platyrrhine and catarrhine dentitions includes on each side of each jaw: two incisors, one canine, two or three premolars and two or three molars. All platyrrhines have three premolars, which was also the ancestral condition in catarrhines, but by the end of the Oligocene the number of premolars in catarrhines had been reduced to two. Most Anthroidea have three molar teeth, but with facial reduction the number of molars is often reduced to two; e.g. in 3–70 % of various races of *Homo sapiens* (Dahlberg, 1951), regularly in marmosets and tamarins, and in the fossil ceboid, *Xenothrix* (Williams & Koopman, 1952). Upper incisors tend to be broad in the Platyrrhini and lower incisors are not specialized except in the Pitheciinae in which they are narrow and elongate and slightly procumbent. (Note the lower incisors of *Cacajao* in Figure 1.) Canines vary in platyrrhines from short and sexually monomorphic to large and highly dimorphic. Male upper canines in the howler monkey, *Alouatta*, are 35 % larger than those of females. This is as great a difference as is found in any of the arboreal African monkeys (Frisch, 1963; Garn, Kerewsky & Swindler, 1966). Upper molars are generally three-cusped in the Callithricidae and four-cusped in the Cebidae; lower molars are generally four-cusped in the Platyrrhini. Platyrrhine molars do not exhibit the bilophodont condition found in the catarrhine monkeys. Enlargement of third molars has occurred independently in both platyrrhines (*Alouatta*) and catarrhines (baboons, gorilla and some colobines).

Three examples of parallelism in the jaws and teeth will be discussed: (a) evolutionary changes in jaw shape, (b) reduction of the cingula, and (c) adaptations to small tough-object feeding.

(a) Jaw shape

One of the more obvious evolutionary parallels in Old and New World Anthroidea is the phylogenetic development of parabolic and parallel-sided jaws. The jaw in primitive (early Tertiary) prosimians was V-shaped with incisors, canine, premolars and molars all in a nearly straight row on each mandibular corpus (Figure 1). Primitive platyrrhines (e.g. *Homunculus*) and unspecialized living platyrrhines (*Cebuella*, *Callithrix*) retained the V-shape. The development of the parabolic hominid and the parallel-sided pongid jaw shape occurred since the Miocene (Kinzey, 1970) and the cercopithecoid jaw became

Figure 1. The parallel evolution of parabolic and U-shaped dental arches in Ceboidea and Hominoidea as seen in occlusal view. The hypothetical Eocene ancestor is reconstructed from omomyines such as *Hemiacodon*; in the absence of relevant fossils, jaw shape of the ancestor of living ceboids is represented by a reconstruction of the Miocene *Homunculus*; *Propliopithecus* represents a probable common ancestor of living hominoids. Among living ceboids *Callithrix* retains the primitive V-shape, and the specialized U-shape occurs in *Cacajao*.



rounded anteriorly since the Miocene (Simons, 1972). The loss of the V-shape occurred irrespective of whether the jaw became shortened (as in hominids) or lengthened (as in the gorilla and baboons) and thus was related to broadening of the anterior portion of the dental arch and not to lengthening or shortening of the face.

Parallel changes have taken place in New World Primates. *Saimiri* has a more nearly U-shaped mandible than its probable Miocene ancestor, *Neosaimiri*, with its V-shaped lower jaw. *Alouatta* has a U-shaped jaw, whereas that of the Miocene *Stirtonia* [considered by Stirton (1951) and Savage (1951) to be closely related to *Alouatta*] is V-shaped. I cannot concur with Hershkovitz (1970b) that *Stirtonia*'s "truncate and compressed symphyseal region" excludes it from an alouattine stem, since lateral expansion of the symphyseal region must have occurred in the alouattine lineage since the Miocene, as it occurred in nearly all other anthropoid lineages except callithricids. The living Pitheciinae, like *Alouatta*, also have U-shaped jaws with large canines. As incisors and/or canines enlarged, the front of the jaw widened creating parallel-sided jaws with large canines (Pitheciinae and Ponginae) and parabolic jaws with small canines (*Callicebus* and *Homo*). This occurred independently in New World and Old World forms since no known Miocene or earlier Primate had parabolic or parallel-sided jaw shape. The parabolic jaw is not specifically a hominid criterion *per se*, but a function of combined factors such as facial shortening and reduction in size (or retention of small size) of anterior teeth—incisors, and especially canines.

Concurrent with change in shape of the lower jaw as seen in occlusal view is a change in the symphyseal angle (Hershkovitz, 1970a), seen in side view. Primitive prosimians have a shallow, nearly horizontal symphyseal angle. In ceboids, as well as in cercopithecoids and hominoids, there is an increase in the angle with a more vertical symphysis in advanced forms. The eversion of the lower anterior border of the mandible, so well known in hominids (Campbell, 1966) is a feature which occurs though to a lesser degree, in ceboids as well. The function of this eversion cannot be related to human speech, erect posture, or reduced anterior dentition, since the same process occurs in forms without these conditions. The eversion of the front of the jaw is functionally related to fusion of the mandibular symphysis, position of the mandibular condyle, and mechanical parameters during the power stroke of mastication.

(b) *The cingulum*

The earliest Primates possessed a cingulum, a well-marked ridge of enamel at or near the base of the crown, on the lingual and buccal sides of upper and on the buccal side of lower premolars and molars. In the earliest known Primate, *Purgatorius* (Van Valen & Sloan, 1965), from Late Cretaceous and Early Paleocene, the upper buccal cingulum was a broad continuous structure, the "stylar shelf." No other Primate possessed such a large shelf (Szalay, 1968); it was reduced to a narrower but still continuous ledge or cingulum in other Paleocene Primates. During the Eocene many of the known prosimians, including some of the Omomyinae, still possessed all three cingula. These structures virtually disappeared in the living Cercopithecoidea, although some remnants of the lingual cingulum were observed by Saheki (1966) in *Macaca fuscata*. Frisch (1965) traced the phylogenetic disappearance of cingula in the Hominoidea; I recently outlined their occurrence and distribution as a morphocline among the living Ceboidea (Kinzey, 1973).

The pattern of distribution of the cingula on molars and premolars of living ceboid Primates suggests a trend of evolutionary reduction, like an *échelle des êtres* in the sense of Clark (1959), following T. H. Huxley. A trend toward reduction was observed by Frisch in the fossil record in three separate evolutionary lines of the Hominoidea. Until such time as the fossil record of the New World Anthropeoidea is better known, the trend postulated on the basis of the morphocline in living forms will serve as a working hypothesis of ceboid dental evolution. In this paper only the upper molar will be considered in detail (Plate 1).

Among the New World Primates the cingula of the marmoset, *Callithrix*, most nearly resemble the primitive Primate pattern. Upper molars possess a complete continuous cingulum on the lingual side and often a complete cingulum on the buccal side [Plate 1(a)]. Lower molars also may possess a complete buccal cingulum around the trigonid, but it is variable. As is typical of Primates generally, the lingual side of lower cheek teeth does not have a cingulum.

Although the general trend in hominoids as well as in ceboids is for the cingulum to reduce, there is one consistent exception in the development of a cusp from the upper lingual cingulum—the hypocone. Evidence for a hypocone is rare in *Callithrix*, but in the tamarin, *Saguinus*, an incipient hypocone may be present [Plate 1(c)]; otherwise the molars of these two callithricids are essentially similar. In *Callicebus*, the titi monkey, generally regarded as the most unspecialized living New World monkey (Gregory, 1922; Clark, 1959; Kinzey, 1971), the hypocone is fully developed and the lingual cingulum

Plate 1. Occlusal views of upper left first molars illustrating a graded series of lingual cingulum reduction in Ceboidea. The mesial side is to the left, the buccal side is at the top. (a) *Callithrix argentata*, (b) *Saguinus oedipus*, (c) *S. mystax*, (d) *Callicebus torquatus*, (e) *Aotus trivirgatus*, and (f) *Ateles paniscus*. [Figure 5 in Kinzey (1973).]



(a)



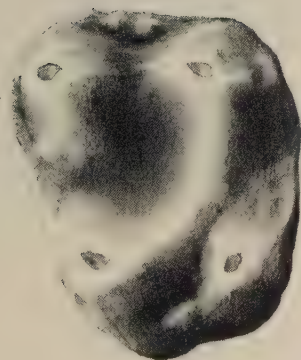
(b)



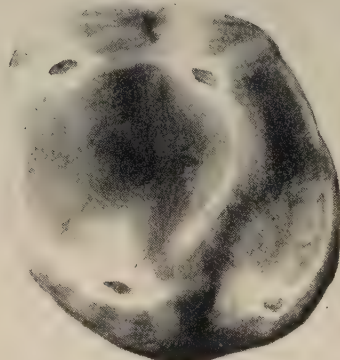
(c)



(d)



(e)



(f)

Plate 2. Buccal view of lower left anterior premolar in *Cacajao rubicundus* (AMNH 76648♀) illustrating buccal cingulum at arrow. Wear from upper canine honing is seen on upper anterior margin of tooth.

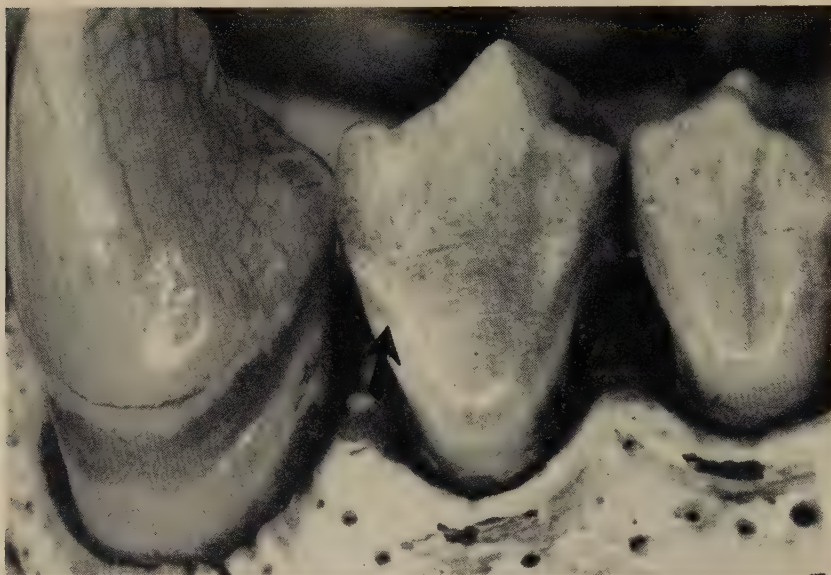


Plate 3. Stereoview of lower anterior premolar in *Oligopithecus savagei* illustrating buccal cingulum. Courtesy of Dr E. L. Simons.

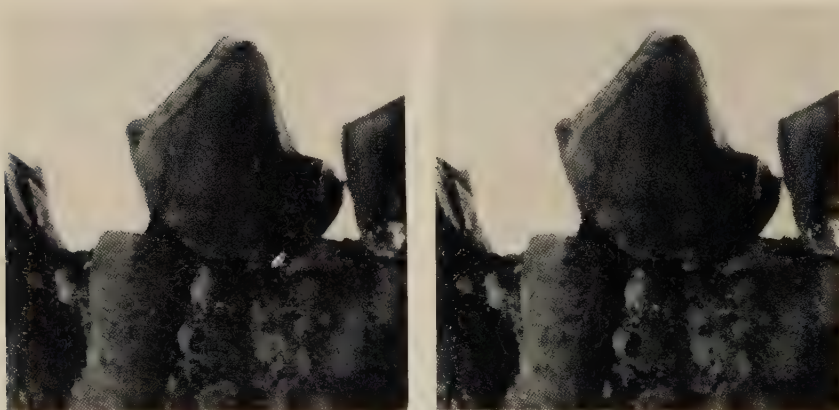


Plate 4. Buccal view of upper left P⁴ and M¹ in *Alouatta senicula* (AMNH 64038) illustrating parastyle and distostyle on both teeth and mesoloph on molar.



Plate 5. Superior view of skulls of *Cebus apella* (AMNH 95320♂) left, and *Cebus capucinus* (AMNH 176632♂) right.

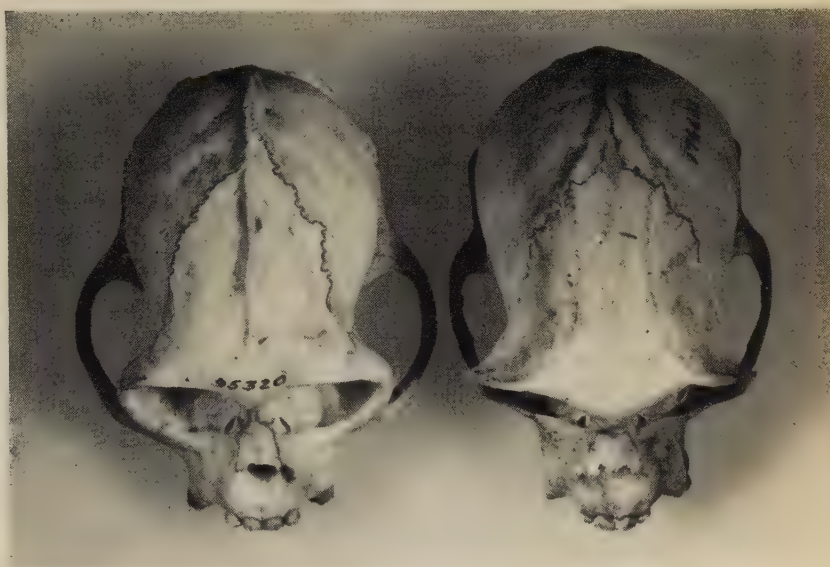


Plate 6. Basal view of same skulls as in Plate 5. *C. apella* is on the left.

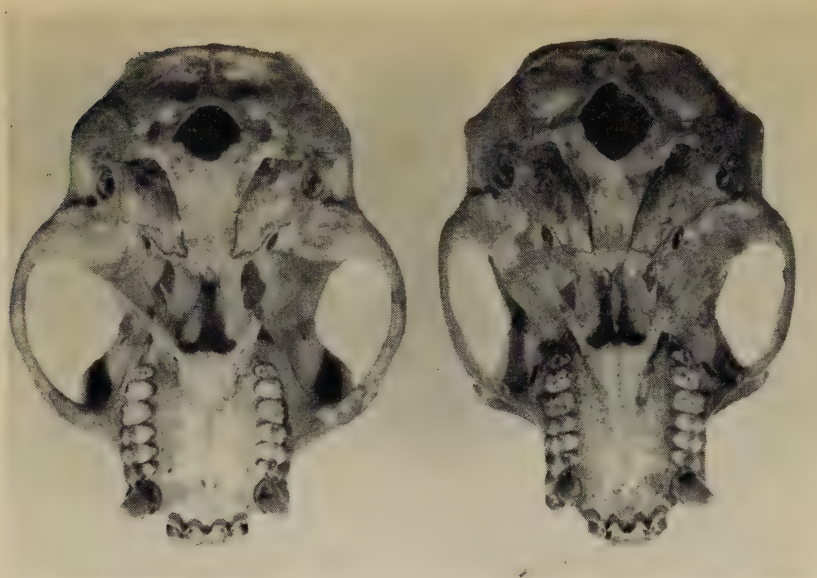


Plate 7. Mandibles of *Cebus apella* (AMNH 94212) above, and *C. capucinus* (AMNH 137993) below.

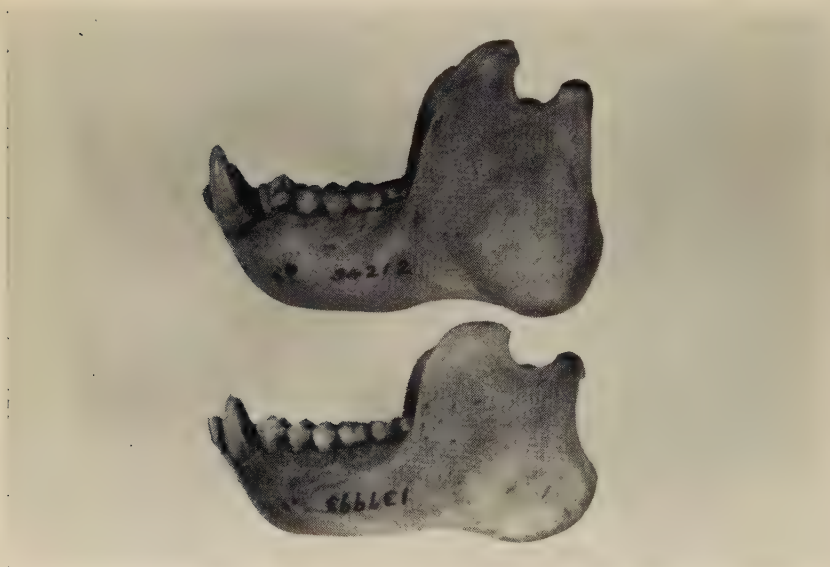


Plate 8. Anterior view of skulls of *Aotus trivirgatus* (AMNH 37500) left, and *Callicebus moloch* (AMNH 72142) right.



Plate 9. Mandibles of same skulls as in Plate 8. *Callicebus* is above.



Plate 10. Anterior view of incisors of *Aotus trivirgatus* (AMNH 36479).

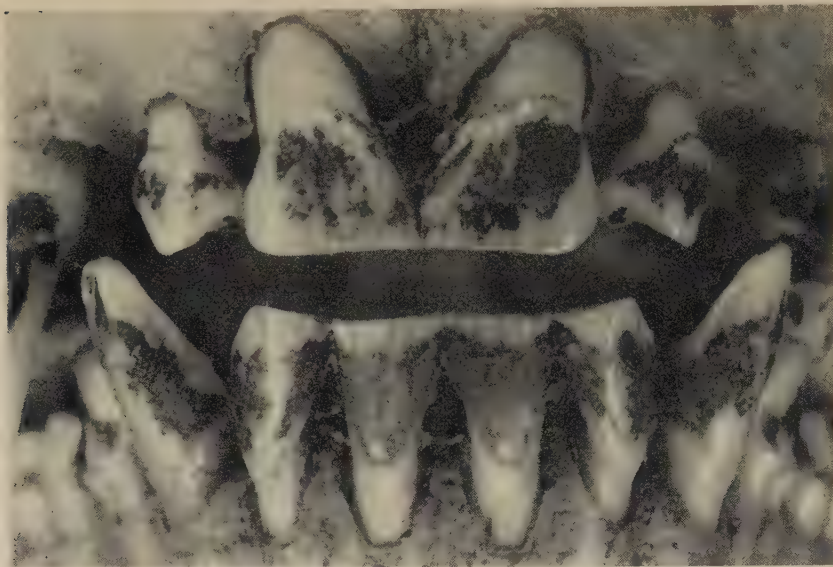
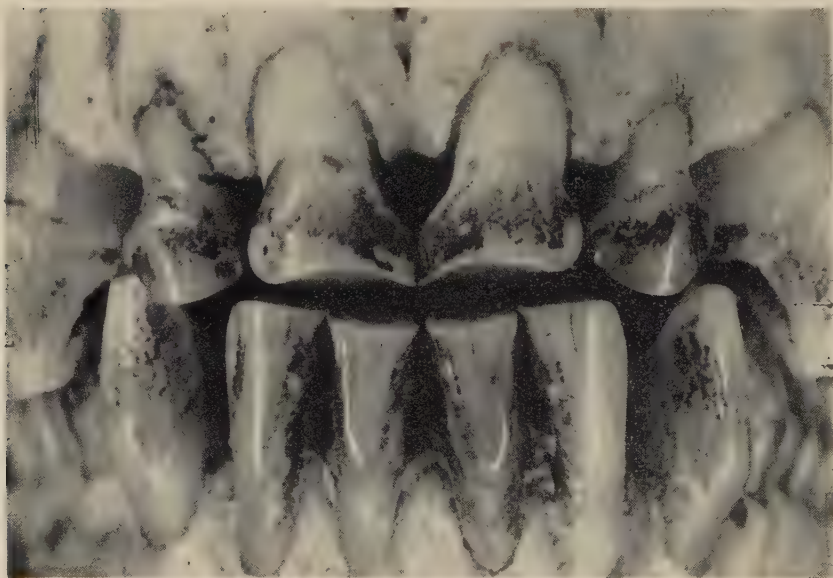


Plate 11. Anterior view of incisors of *Callicebus torquatus* (AMNH 76926).
Note difference in incisal wear from that in *Aotus*.



from which it arose is still completely present [Plate 1(d)]. The buccal cingulum is no longer a continuous structure but remains only in the form of small styler cusps, variously present.

In the Pitheciinae (Saki monkeys and the Uakari) the upper lingual cingulum is also broken up into separate cusps rather than remaining as a continuous structure, and the upper buccal cingulum is virtually lost. Last of all Atelinae, including the spider and woolly monkeys but probably excluding *Brachyteles* (Zingesser, 1972), in most cases have lost all traces of cingula on the molars and premolars [Plate 1(f)].

The general trend in Ceboidea has been for the upper buccal cingulum to be lost first, the lower buccal cingulum to be lost next, and the upper lingual cingulum to be lost last. This is readily understandable in terms of occlusal relationships, and the trend is probably related to functional changes in the masticatory apparatus associated with dietary changes from insectivorous to frugivorous feeding. The retention of a primitive pattern in the cingula of the squirrel monkey, *Saimiri*, can thus be related to its rather highly (for a monkey) insectivorous diet. The trend of cingulum reduction is paralleled in the Hominoidea, as represented in the fossil record for the hominids, pongids, and hylobatids: the buccal cingula are lost first and the lingual cingulum last. [Slight differences in the pattern of reduction were noted previously (Kinzey, 1973).]

Is the knowledge of general trends in cingulum reduction of value in understanding catarrhine evolution? Three examples will be given. First, the enigmatic Late Miocene *Oreopithecus* has well-developed cingula on upper premolars and molars, as well as on lower molars. One would therefore predict, if the trend is followed, that any predecessor of *Oreopithecus* would also have buccal cingula. *Apidium* from the Fayum Oligocene has the requisite cingular structures in both its upper and lower dentitions to have been predecessor to *Oreopithecus*. Thus, additional evidence is provided for their phylogenetic relationship.

In addition to the general trend toward cingulum reduction in Ceboidea, two other features of the cingulum should be mentioned. While the pattern of cingulum reduction seems fairly well established for the molars and the posterior premolars, the anteriormost premolar in the lower jaw of ceboids follows a different pattern. Briefly, its buccal cingulum is related to the presence or absence of canine honing, that is, the shearing of the upper canine tooth against the lower anterior premolar. The incidence and development of the buccal cingulum on the anterior premolar in the Ceboidea is least in those animals with the smallest canine teeth: *Callithrix* and *Callicebus*. It is strongly developed in *Saguinus*, *Saimiri*, *Cebus*, and the Pitheciinae, all of which have large upper canine teeth (Plate 2). Only in the large platyrrhines such as the howler, spider and woolly monkeys, does the functional requirement for this buttress on the anterior lower premolar disappear, presumably because of the absolutely large size of the tooth. This cingular structure is absent from all living catarrhine Primates, presumably due to the larger size of the tooth and to the differing nature of canine honing in catarrhines. In the Fayum Oligocene, however, the earliest known hominoid, *Oligopithecus*, whose lower jaw is considerably smaller than that of any living catarrhine, has a lower anterior premolar that shows evidence of the honing mechanism (Simons, 1972). Consistent with its small size and the presence of the honing mechanism, a small buccal cingulum is present on the anteriormost premolar (Plate 3).

Another feature in the cingulum of Ceboidea which does not follow the general pattern of reduction is the presence, in *Alouatta* (and occasionally in *Brachyteles*, Gregory, 1920,

p. 219) of highly developed derivatives of the buccal cingulum on upper premolars and molars. The cingulum in *Alouatta* is not a continuous structure, but a series of three buccal styler cusps on the molars and two on the premolars (Plate 4). Since a similar dental feature is generally associated with a leafy diet (e.g. similar structures are found in the marsupial koala bear, and in the Madagascar lemuroid Indriidae) one might expect similar structures in the Old World leaf-eating colobines. Such structures, however, have not been noted. Apparently the trend of cingulum loss, which proceeded farther and more rapidly among Cercopithecoidea than in any other Primate superfamily, precluded the retention or enlargement of upper buccal cingula. From a functional point of view the colobines may have insufficient lateral mandibular excursion to require buttressing of upper buccal cusps with external cingula and mesostyle, as in the case of *Adapis* compared with *Notharctus* (Gregory, 1920); or, the direction of mandibular movement during the buccal phase of chewing in colobines may be more like that of *Adapis* (Gingerich, 1972) which lacks a mesostyle, and quite unlike that of *Alouatta* which has a mesostyle or mesoloph. The buccal surface of the protoconid and hypoconid of M_1 has a greater extent of wear in *Alouatta* than in *Colobus* indicating development of greater lateral stress in the former against the metacone and paracone respectively. These cusps apparently require buttressing by well-developed buccal cingula and mesoloph in *Alouatta* but not in *Colobus*. Resolution of the problem of buttressing upper buccal cusps requires further comparison of molar occlusion in *Alouatta* and the colobines.

Developed upper buccal cingula, while absent from living catarrhines, may be found in one fossil form—*Oreopithecus* (Butler & Mills, 1959). *Oreopithecus* has styler cusps or ledges on upper premolars and molars. On the basis of this evidence *Oreopithecus*, like *Alouatta*, probably was a specialized leaf-eater as was suggested by Coon (1963) on the basis of other criteria of the face and jaws. The presence of a metaconule and its related crest provides an additional shearing edge, advantageous to masticating such a diet.

(c) *Small tough-object feeding*

One of the significant contributions to our understanding of morphological features in the hominoid masticatory apparatus is C. J. Jolly's analysis of small-object feeding. Similar adaptive patterns have been described in the teeth and jaws of the gelada baboon, robust australopithecines, the lemuroid *Hadropithecus*, *Gigantopithecus*, and the mountain gorilla (Jolly, 1970a,b; Groves, 1970). The complex, as described by Jolly, involves two basic behavioral adaptations—"extreme terrestriality and a diet of small, tough, food-objects." It is my contention that these two adaptations need not occur together, but may occur sequentially in the evolutionary process. To demonstrate this it is necessary to show first that the adaptive features of small-object feeding may occur in an arboreal habitat. Two examples will be chosen from the New World monkeys, utilizing an intrageneric comparison, and an intergeneric one.

As a result of the taxonomic review of Hershkovitz (1949) the species of the capuchin monkey, *Cebus*, are readily distinguishable. Only one species, *C. apella*, has a complete sagittal crest, and most other differences among the species are in the pelage. No previous attempt has been made to understand functional differences between the skull of *C. apella* and those of the other species. *C. apella* and *C. capucinus* will be examined as they are the most extreme forms; the other two species are intermediate in form (although they are more like the latter.) The dentition of *C. apella* is adapted for powerful crushing of objects,

Table 1.

Dental measurements in two species of *Cebus*

	N	I ¹		M ¹		M ₁	
		Length	Breadth	Length	Breadth	Length	Breadth
<i>C. apella</i>	26	4.14 ± 0.05	4.00 ± 0.04	4.50 ± 0.04	6.04 ± 0.05	4.88 ± 0.04	4.91 ± 0.05
<i>C. capucinus</i>	26	4.35 ± 0.04	4.10 ± 0.03	4.26 ± 0.04	5.60 ± 0.06	4.63 ± 0.03	4.66 ± 0.04
% difference		-5.0%	-2.6%	+5.5%	+7.9%	+5.6%	+5.5%
Significance		<0.01	<0.025	<0.001	<0.001	<0.001	<0.001

N = sample size; measurements in mm; mean ± s.e.

perhaps small objects, between the large first and second molars (Table 1). (Oddly enough the third molar is consistently larger in *C. capucinus*.) The zygomatic arch is wide and the skull has a marked post-orbital constriction to accommodate a large temporalis muscle which may form a sagittal crest; the temporalis is set forward on the cranium and the zygomatic arch joins the face opposite the last premolar and first molar; the ascending ramus of the mandible is vertical and the condyle is high above the occlusal plane; the mandibular body is thick under the molars (Plates 5-7). In contrast *C. capucinus* does not have as marked post-orbital constriction, nor a sagittal crest on the anterior part of the skull; the zygoma meets the face opposite the second molar; the ascending ramus of the mandible is less vertical, the condyle is closer to the level of the occlusal plane, and the central maxillary incisors are broader and have longer roots. The dentition of the latter species (except for a larger functional third molar) appears to be better adapted for incisal preparation of food and less well adapted for chewing hard tough objects. The diet of *C. capucinus* has been studied by Hladik *et al.* (1971) and they note that 65% of the diet is composed of fruits of various plants, 15% of foliage and 20% of insects and animal prey. No detailed studies of the diet of *C. apella* have been carried out, although there are reports in the literature of eating small nuts, cocoa beans and mulberry seeds (Hill, 1960). The two species are apparently sympatric in parts of their range and I predict that a detailed study of the two species would show marked dietary displacement substantiating the morphological adaptations mentioned above. The significance of this will be noted below.

A second comparison is made between the titi monkey (*Callicebus*) and the night monkey (*Aotus*) which are closely related South American genera. They are similar in cranial characteristics, except for the orbital expansion in *Aotus* (in conjunction with its adaptation for nocturnal vision) and the expansion of the angle of the jaw in *Callicebus*. Although canine, premolars, and molars are morphologically similar in the two genera, canines are sexually dimorphic in *Aotus* and not in *Callicebus moloch* (Kinzey, 1972). Other functional differences in the dentition may also be observed (Plates 8-11). In *Callicebus* the incisors, particularly the central incisors, are smaller than those of *Aotus*; the canines are small, the dental arcade narrows anteriorly, the basioccipital is short and broad, the ascending ramus of the mandible is vertical, the molar cusps are set wide apart, the premaxilla is reduced and the premaxillary suture closes early. Opposite features are found in *Aotus*. Consistent differences have not been observed in post-orbital constriction or position of the temporal lines on the skull, but differences may be obscured by the enlarged orbits in *Aotus*.

Microscopic examination of the teeth shows a very different utilization of incisors in *Callicebus* and *Aotus*. The incisors in *Aotus* wear heavily and flat from marked utilization

(Plate 10). In *Callicebus* the incisors generally are much less worn, but when they do wear the occlusal edges incline from front to back (Plate 11), as though they were used for pulling something across them, perhaps to remove the husks from seeds.

The diets of *Aotus* and *Callicebus* are not well known. *Aotus* eats a variety of fruits and insects, according to Moynihan (1964), and food is seized with the front teeth and not with the hands. In contrast *Callicebus* handles food with its hands before eating (Moynihan, 1966) and Mason (1970) states that *Callicebus* does "take in considerable quantities of tough vegetable matter" and it also "extracts seeds from pods . . ."

Cebus, *Callicebus* and *Aotus*, as all New World Primates, are arboreal. They rarely come to the ground. Yet, *Cebus apella* and *Callicebus* are morphologically adapted for small tough, object-feeding. The complex of characteristics that Jolly describes, sometimes called the T-complex (Simons & Ettel, 1970), is really at least two sub-complexes—one involving small-object feeding and found in *Cebus apella* and *Callicebus*, the other involving terrestrial adaptation. Both sub-complexes occur together in the gelada baboon and in early Pleistocene hominids, but they did not necessarily evolve together. Groves (1970) very wisely distinguished between the functional complex in *Gigantopithecus* and the mountain gorilla, and "the ultimate elaboration of the T-complex . . . (which) is characteristic of Man and *Theropithecus* alone." This is a valid distinction. The functional complex (of small-object feeding) is found in two New World monkeys which, however, have not attained its ultimate elaboration by becoming terrestrial. *Callicebus* and *Cebus apella* represent platyrrhine morphological adaptations to small, tough object-feeding in an arboreal habitat. Behavioural aspects of the adaptation require verification in the wild.

3. Significance of Parallelism for Human Evolution

The following characteristics are among those generally considered diagnostic of the Hominidae: small canine and incisor teeth, anteriorly converging dental arcade, homomorphic lower premolars, mandible with shallow body thickened bucco-lingually under the molars, and basi-occipital short and broad. This pattern is contrasted with that of living pongids which is characterized as having: large incisors and large sexually dimorphic canines, U-shaped dental arcade, heteromorphic lower premolars, a deep body on the mandible, and a narrow basi-occipital. The former sub-complex of features, found in the hominids, is also found in *Callicebus* and (for the most part) in *Cebus apella*. This sub-complex is associated with the behavioural adaptation to tough, small-object feeding, and in the New World occurs in an arboreal habitat, while the entire, fully elaborated T-complex is found only in gelada baboons and in early Pleistocene hominids, associated with terrestrial truncal erectness.

The significance of these remarks for human evolution is that the dichotomy observed between hominids and pongids in adaptive dental features may arise in an arboreal environment. This means that while the adaptive significance of the fully elaborated T-complex for the origin of terrestrial activity in early hominids is not denied, it is highly possible that the dental features alone may have occurred first in the earliest hominids in an arboreal environment, presumably during the Miocene. To put it another way, Jolly's Phase I hominid has features which could have evolved initially in an arboreal habitat, with a subsequent adaptation to terrestrial feeding.

The dental features of *Ramapithecus*, insofar as they are known, exemplify this sub-complex of dental characteristics. Tattersall (1969a,b) has shown that the fauna associated with *Ramapithecus* "pre-date the widespread development of open savanna fauna" and that *Ramapithecus* was most likely a forest-dwelling Primate. The presence of the sub-complex of T-complex features associated with arboreal feeding is consistent with this view. Many anthropologists have sought (in vain) for possible evidence of terrestrial adaptation in *Ramapithecus* on the assumption that the initial adaptation of hominids was for terrestrial bipedalism. Jolly (1970a) as well as Simons (1972) visualize *Ramapithecus* looking for seeds on the ground in or at the edge of the forest. The only known distinction between *Ramapithecus* and its contemporary hominoids is in the jaws and dentition (since these are the only remains known). When postcrania are found I predict that unlike the more recent australopithecines they will not show evidence of adaptation to terrestriality. The basic initial adaptation of the Hominidae was probably dietary in an arboreal habitat, and with the increasing availability of savanna habitat high selective value was placed upon the full-blown Phase I adaptation to terrestrial small-object feeding.

In conclusion it is evident that the study of parallel developments in the dental apparatus of the platyrrhine Primates has a place in the interpretation of catarrhine evolution, including hominid evolution. The recent evidence that Old and New World monkeys may be more closely related than was previously supposed, if valid, increases the significance of inferences from the Platyrrhini to the Catarrhini.

I am grateful to E. L. Simons for the stereo photographs of *Oligopithecus* and for permission to examine original specimens of *Apidium*, and to A. L. Rosenberger and E. E. Hunt, Jr. for critical comments and suggestions. I am also indebted to the Department of Mammalogy, American Museum of Natural History for permission to use its facilities.

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Irwin S. Bernstein

Department of Psychology,
University of Georgia,
Athens, Georgia 30602, U.S.A.

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Birth of Two Second Generation Hybrid Macaques

A male infant was born to a hybrid female monkey (*Macaca mulatta* $\times$ *M. nemestrina*) on 24 May 1973. On 4 July 1973, a second hybrid female macaque (*M. nemestrina* $\times$ *M. nigra*) also produced a viable female infant. These were the twenty-seventh and twenty-eighth hybrid births in our program, but the first second generation births.

Inasmuch as some measure of genetic isolation is essential to any definition of species, births of hybrid animals pose taxonomic problems. A wide variety of hybrid monkeys have been reported (Gray, 1971) both in captive colonies (where such births may be attributed to artificial conditions even if resulting from natural mating) and in wild populations (Aldrich-Blake, 1968; Bernstein, 1966; Fooden, 1971). The existence of hybrids does not in itself demonstrate gene flow between populations, but evidence of hybrid fertility suggests this possibility. The report of a "hybrid zone" between two species of baboon (*Papio*) (Nagel, 1971) thus was taken by some as strong support for suggestions to reduce these populations to subspecific standing.

The production of second generation hybrids involving widely divergent macaque species suggests that such evidence alone is not the *sine qua non* for subspecific reduction. On 24 May 1973, a female hybrid (*Macaca mulatta* $\times$ *M. nemestrina*) gave birth to a viable male infant. On 4 July 1973, a female hybrid (*Macaca nemestrina* $\times$ *M. nigra*) also produced a viable female infant. The presumed father, born 11 November 1964, is himself a hybrid (*M. fascicularis* $\times$ *M. nemestrina*), although pending biochemical paternity tests it is not possible to eliminate the pigtail monkey half sibling (born 4 April 1968) of the first female as a putative father. Respective birthdates for the two females are 11 April 1967 and 17 September 1968.

Normal maternal care has been noted despite the fact that the first of these primiparous females was hand reared by the author from week five to age six months. The cause of initial rejection was undetermined, but from that date, until introduction to the hybrid group at age six months, there had been no opportunity for social interaction with monkeys. The only lapse in maternal care resulted from attempts to examine the infant by isolating mother and infant in a small cage. Normal maternal care resumed after mother and infant were successfully reunited by releasing both animals back into the group. Both infants have received considerable attention from other group members including handling and carrying.

The present births are the twenty-seventh and twenty-eighth live hybrids produced in the program. All hybrids have been within genera and include: 2 in *Cercopithecus* (guenons) 1 in *Ateles* (spider monkeys), 4 in *Mandrillus* (drills and mandrills), 3 in *Cebus* (capuchins) and 19 in *Macaca* (macaques). Whereas some of the species involved might be argued to be only subspecies, such argument seems weak for the variety of macaques

involved and for such cases as vervets with Sykes monkeys, where chromosome numbers differ.

Although the present infants are the first second generation live births in our colony, it should be noted that back crossing a female *M. fascicularis* $\times$ *M. nemestrina* to the paternal species has resulted in two conceptions, the last of which resulted in a well formed still born infant.

Even should it prove possible to routinely produce fertile hybrid monkeys in the laboratory, I would not argue for a revision of present taxonomy. Inasmuch as evolution is a dynamic ongoing process, we must expect life forms to represent every "stage" of speciation and acknowledge that such a continuum will defy discrete classification systems. Furthermore, since selection for separation of population gene pools can only take place where there is genetic exchange between populations, the existence of any effective mechanism barring hybridization eliminates selective pressure to further develop other potential isolating mechanisms. Any drastic change which thwarts the existing separation mechanism in no way alters the history of natural selection which produced the species we recognize in their natural habitats.

The production of second generation hybrid macaques is, therefore, not presumptive evidence for lumping all the macaques into a single species. Far too much information concerning species differences and phylogenetic history would be lost in communications using traditional binomial nomenclature.

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W. Leutenegger

*Department of Anthropology,
University of Wisconsin,
Madison, Wisconsin, U.S.A.*

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Functional Aspects of Pelvic Morphology in Simian Primates

In functional analyses of the Primate pelvis only selective forces resulting from locomotory functions have traditionally been taken into account, therefore neglecting possible selective forces resulting from obstetrical functions. This paper analyzes the nature, degree, and action of the selective forces acting on the pelvis of simian Primates which result from maternal-fetal size relationships and their interaction with selective forces resulting from locomotory functions. Based on the analysis of these factors in living Primates, an estimate of their degree and interaction in *Australopithecus africanus* is given to further elucidate the problem of the evolution of hominid bipedalism.

1. Introduction

After some decades of stagnation in the field of functional morphology and biomechanics, there has been re-established in recent years a trend toward studying skeletal morphology from a functional viewpoint. In primatology, initiators of this trend were Erikson (1952, 1960, 1963), Oxnard (1963), and Ashton & Oxnard (1964*a,b*), in the 1950s and early 1960s. In analyzing the postcranial skeleton, particularly the limb bones, these authors and later numerous other investigators proceeded by (1) classifying Primates into discrete locomotor categories on the basis of behavioral studies, and by (2) relating locomotor differences to differences in structural and metrical features of certain regions of the postcranial skeleton. Since the appendicular skeleton primarily serves locomotory functions, more or less close relationships between a certain mode of locomotion and morphological features could be demonstrated in these analyses.

A functional analysis of the pelvis requires another approach. In contrast to the other postcranial regions, the pelvis serves not only locomotory functions, but also obstetrical functions. In analyses of the Primate pelvis from a functional viewpoint, it is an astonishing fact that, with a few exceptions (Waterman, 1929; Washburn, 1951, 1963; Leutenegger, 1970*a,b*, 1972*a*; Robinson, 1972; Lovejoy *et al.*, 1973), possible selective forces resulting from newborn size in relation to maternal size, which also influence pelvic morphology, have not been taken into account. Similarly, some of the most recent papers studying the pelvic region of early hominids have dealt with the question of how efficient these Primates were with regard to bipedal locomotion (Jenkins, 1972; Robinson *et al.*, 1972; Sigmon, 1971; Zihlman, 1971; Zihlman & Hunter, 1972), without taking into account the possible selective forces resulting from maternal-fetal size relationships.

It has been demonstrated (Leutenegger, 1970*a,b*, 1972*a,b*) that, regarding construction of the pelvis, selective forces based on locomotory functions are opposed by those resulting from obstetrical functions. Furthermore, selective forces based on locomotory functions, to minimize the distance between sacroiliac- and hip-joint, are dependent on the mode of locomotion, and the selective pressure for enlargement of the female pelvic canal to ensure parturition also varies interspecifically. This suggests that also the interaction between these forces must vary interspecifically.

This paper will try to analyze the nature, degree, and action of the selective forces acting on the Primate pelvis which result from maternal-fetal size relationships and their interaction with selective forces resulting from locomotory functions. Based on the analysis of these factors in living primates, an estimate of their degree and interaction in *Australopithecus africanus* will be presented to further elucidate the problem of the evolution of hominid bipedalism.

2. Newborn Size and Female Pelvic Dimensions

Living Primates

Successful delivery in mammals is mainly dependent on the size relationship between the dimensions of the head of the fetus at term and those of the pelvic inlet of adult females. Schultz (1942) recognized that among Primates these relationships vary widely interspecifically. He noticed that in certain Primates (e.g. pongids) the main diameters of the female pelvic inlet are strikingly larger than those of the newborn's head, thus permitting an easy delivery, while in other Primates (e.g. macaques, modern Man) there is an amazingly small difference between the corresponding dimensions of the female pelvic inlet and those of the newborn's head, one which barely permitted delivery.

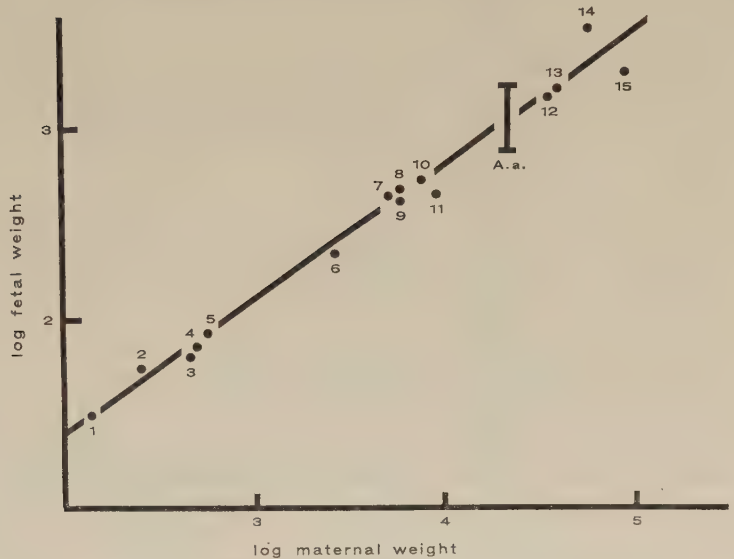
The head size of the fetus at term and its relationship to the dimensions of the female pelvic inlet is dependent on 2 main factors (Leutenegger, 1970c): (1) size of the fetus at term relative to the size of the mother, and (2) degree of encephalization at birth.

Maternal-fetal size (weight) relationships in Primates are currently under detailed investigation (Leutenegger, 1974). However, some preliminary results can be presented. As has been demonstrated (Leutenegger, 1972b) in simian Primates, maternal and fetal (birth) weights are in allometric relationship. Fetal weight (F) is given in terms of the initial size constant (b) and the maternal weight (M) raised to an exponent a (constant of allometry). Thus, $F = b \cdot M^a$, or $\log F = \log b + a \cdot \log M$. This has been tested by plotting $\log F$ against $\log M$ for 15 extant species of simian Primates, based on data from Schultz (1949, 1956), Napier & Napier (1967), and Leutenegger (1970c) (Figure 1). Fetal weight is considered to be the weight of the entire litter if there is more than one offspring, which is true for all species of callithricids (numbers 1-4 in Figure 1). The least squares equation is $\log F = 0.70 \log M$, or $F = M^{0.70}$. The initial size constant is $\log b = 0$, or $b = 1$. The correlation coefficient is 0.98. Since the constant of allometry is less than 1 (negative allometry), this indicates that Primates of small adult body size have relatively larger newborns than Primates of larger adult body size. Newborn gorillas, however, are exceptionally small, whereas human newborns are strikingly larger than expected on the basis of the regression.

Data on the degree of brain development at birth are rather scanty. From the few published data (Schultz, 1940, 1941, 1956; Leutenegger, 1970c) it can be inferred that, as a general rule, newborns of small-sized Primates have larger brains relative to their body weight than larger Primates. This indicates that interspecific brain-body size relationships in newborn Primates represent a negative allometric function, probably very similar to the relationships in adult Primates.

Since maternal-fetal size relationships as well as newborn brain-body size relationships represent negative allometric functions, the addition of these two factors results in newborn cranial dimensions of small-sized Primates generally much larger relative to maternal size than in larger-sized Primates. There are, however, exceptions to this rule which will be discussed.

Figure 1. Maternal-fetal (birth) weight relationships in 15 extant species of simian Primates, and 95% confidence interval of expected mean birth weight for *Australopithecus africanus* (A.a.). The log of the mean maternal weight is plotted against the log of the mean birth weight, and the least regression is drawn. Numerical designation of species: 1 *Cebueella pygmaea*, 2 *Callithrix jacchus*, 3 *Saguinus tamarin*, 4 *Saguinus oedipus*, 5 *Saimiri sciureus*, 6 *Cebus capucinus*, 7 *Lagothrix lagothricha*, 8 *Alouatta villosa*, 9 *Macaca mulatta*, 10 *Ateles geoffroyi*, 11 *Nasalis larvatus*, 12 *Pongo pygmaeus abelii*, 13 *Pan troglodytes*, 14 *Homo sapiens*, 15 *Gorilla gorilla*.



With the information on the factors influencing the cranial dimensions of newborns, their relationship to the dimensions of the female pelvic inlet can be analyzed. Data on main diameters of the pelvic inlets of adult females and corresponding dimensions of the heads of newborns are presented in Table 1. Since in non-human Primates the median-sagittal plane of the fetal head enters the pelvic canal aligned with the median-sagittal plane of the pelvis, and the head does not undergo rotation during passage through the pelvic cavity, the critical dimensions for a successful delivery are therefore the ratios between total head height and sagittal diameter of the pelvic inlet and between head breadth and transversal diameter of the pelvic inlet.

It is important to note that in the sagittal plane head length is not as vitally important as total head height (= projective distance between vertex and gnathion), because during parturition the head can be tilted into a dorsoflexed position, so that the face, which in the sagittal direction is shorter than the neurocranium, enters the pelvic inlet first. Strong dorsoflexion of the head during parturition must be particularly important in callithricids, small cebids, and probably most cercopithecoids, because if the neurocranium entered the pelvic inlet first, the head could not pass successfully through the pelvic canal. In the large cebids, hylobatids, and pongids, the sagittal diameter of the female pelvic inlet significantly exceeds newborn head length and also total head height, indicating that in these Primates the dimensions are not of vital importance during parturition.

Table 1
Means (mm) of main diameters of the female pelvic inlet, means (mm) of main cranial dimensions of newborns, and their mutual relationships. Data based on Schultz (1949) and Leutenegger (1970*b,c*)

Species	Adult females			Newborns			Relative head size		
	<i>n</i>	Sagit. diam.	Trans. diam.	<i>n</i>	Head length	Head height	Head length in % sagit. diam.	Head height in % sagit. diam.	Head breadth in % trans. diam.
<i>Callithrix jacchus</i>	15	19.7	17.2	4	27.9	20.3	141.5	103.0	104.5
<i>Saimiri sciureus</i>	7	29.4	23.1	3	40.0	32.0	136.0	108.9	121.1
<i>Cebus capucinus</i>	4	45.3	35.1	2	52.5	46.0	116.0	101.5	118.2
<i>Alouatta villosa</i>	2	70.0	47.0	1	48.0	43.0	68.6	61.4	80.8
<i>Lagothrix lagothricha</i>	4	80.5	44.3	1	61.0	52.0	74.8	64.6	114.4
<i>Ateles geoffroyi</i>	7	90.3	54.4	8	66.9	60.9	74.0	67.4	112.1
<i>Macaca mulatta</i>	41	67.7	50.9	28	66.3		98.0		99.6
<i>Nasalis larvatus</i>	15	71.5	51.8	1	64.0		89.5		94.6
<i>Hylobates lar</i>	87	78.7	55.9	6	64.2		81.6		94.3
<i>Pongo pygmaeus</i>	26	149.6	102.5	4	84.1		56.2		73.1
<i>Pan troglodytes</i>	29	149.5	98.0	9	83.0		55.5		72.4
<i>Gorilla gorilla</i>	10	175.7	122.6	4	97.0		55.3		64.4
<i>Homo sapiens</i>	10	112.9	121.6	10	123.8		87.4*		101.8†
<i>Australopithecus africanus</i>	1	85.0	99.0						

* Head breadth in % of sagittal diameter.

† Head length in % of transversal diameter.

The ratio between newborn head breadth and transversal diameter of the female pelvic inlet varies interspecifically at least as markedly as do the ratios in the median-sagittal plane (Table 1). In all the platyrrhini except the howler monkey, the mean head breadth is larger than the mean transversal diameter of the pelvic inlet. The relative smallness of the head of newborn howler monkeys is clearly due to an exceptionally low degree of brain development, and not to a low birth weight. Relative cranial capacity of newborn howler monkeys has been estimated at 7% (Leutenegger, 1970c) which is significantly below the values of all other simian Primates investigated so far. However, with regard to maternal-fetal weight relationship, the howler monkey is not at all exceptional (Figure 1).

The largest cranial dimensions in newborns compared to female pelvic dimensions are found in the squirrel monkey. The enormous head size of newborn squirrel monkeys is primarily due to an exceptionally high degree of brain development at birth, when cranial capacity reaches approximately 18% of the body weight (Leutenegger, 1970c). In addition, newborn cranial dimensions in the squirrel monkey are also influenced by the relatively large overall size of the newborns; average birthweight is close to $\frac{1}{7}$ of the average weight of adult females. Among the catarrhini, in cercopithecoids and hylobatids, mean newborn head breadth is only slightly smaller than the transversal diameter of the pelvic inlet, whereas in pongids the latter is markedly larger.

Since in all the platyrrhini (except the howler monkey), cercopithecoids, and hylobatids, one or the other of the newborn cranial dimensions exceeds or comes close to the corresponding diameter of the female pelvic inlet, there can be no doubt that in these Primates successful delivery is only possible by dilatation of the pelvic ligaments shortly before and during parturition. Despite dilatation of the pelvic ligaments, however, labor can be strenuous and delivery difficult, as has been reported for callithricids (Christen, 1968), squirrel monkeys (Bowden *et al.*, 1967; Hopf, 1967; Goss *et al.*, 1968), baboons (Gillman & Gilbert, 1946), and rhesus macaques (Brandt & Mitchell, 1971). Furthermore, abortions, miscarriages, and stillbirths are quite frequent among these Primates (cf. Brandt & Mitchell, 1971). In squirrel monkeys, for example, in whom the cranial dimensions of newborns are the largest compared to female pelvic dimensions, less than 50% of the fetuses survive birth (Goss *et al.*, 1968). In howler monkeys and pongids, on the other hand, the cranial dimensions of newborns are markedly smaller than the corresponding diameters of the female pelvic inlet. Studies on delivery behavior of the howler monkey have not been reported yet, but for pongids delivery has been reported to be quick and easy and labor often hardly even detectable (Brandt & Mitchell, 1971).

In contrast to the non-human Primates, in modern Man the sagittal diameter of the pelvic inlet has become shortened so as to be significantly smaller than the transversal diameter. This is a result of the dorsocaudal rotation of the sacroiliac-joint as an adaptation to habitual bipedalism. During the entry of the fetal head into the pelvic cavity, the median-sagittal plane of the head is therefore aligned with the transversal plane of the pelvic inlet. However, since the sagittal dimension of the exit of the pelvic cavity is larger than the transversal dimension, the fetal head has to undergo a rotation of 90 degrees when passing through the pelvic cavity. With regard to the size relationship between newborn cranial dimensions and female pelvic dimensions, the situation in modern Man is very similar to that in ceboids and cercopithecoids; that is to say, there is only a very slight difference between the corresponding cranial and pelvic dimensions.

Contrary to the traditional view, however, the relatively large head size of human newborns is not primarily the result of a particularly enlarged brain. Average relative cranial capacity in newborn humans (9.9%; Schultz, 1941) is only slightly larger than in newborn chimpanzees (9.7%, based on data from Schultz, 1940, 1941). Rather, it is the disproportionately large overall size of the newborn (Figure 1) which causes the relatively large cranial dimensions.

Fossil Primates

Size relationships between cranial dimensions of newborns and female pelvic inlet dimensions need not only be studied in living Primates; it is also possible to come up with reasonable estimates of these factors for fossil Primates. Of particular significance with regard to the evolution of hominid bipedalism are estimates on newborn head size in relation to the size of the female pelvic inlet in australopithecines. Although quite complete pelvic remains are known from both *A. africanus* and *A. robustus*, pelvic inlet dimensions have been reported only for *A. africanus* (STS 14) (Leutenegger, 1972*b*). In STS 14, which represents a mature, possibly female individual (Robinson, 1971), the sagittal diameter of the pelvic inlet measures 85 mm, and the transversal diameter 99 mm. Since pelvic inlet dimensions are known of *A. africanus* only, it seems appropriate to discuss in this paper estimates of newborn size of this particular hominid only. Information on newborn size of *A. robustus* is presented elsewhere (Leutenegger, 1972*b*).

An estimate of cranial dimensions of newborn *A. africanus* can be obtained based on corresponding data from living Primates. As demonstrated in this paper, cranial dimensions of newborn Primates are depending on two main factors: (1) newborn body size, which can be best expressed in birth weight, and (2) degree of brain development at birth.

As already demonstrated, in simian Primates maternal and fetal (birth) weights are in allometric relationship, constituting a regression equation of $F = M^{0.70}$. Since, from a regression equation, F for any given M can be predicted, these data combined with estimates on maternal body weight of *A. africanus* provide a means for the estimation of the birth weight for this hominid. Estimates of body weight for adult australopithecines have usually been based on dimensions on robusticity of postcranial remains. Body weight for STS 14 has been estimated at 50 lb (Robinson, 1971) with a possible range of 40 to 70 lb (Pilbeam, 1972). Based on a maternal weight of 22,500 g (= 50 lb) and on the above mentioned regression equation, the birth weight of *A. africanus* can be estimated. In Table 2 the expected mean birth weight of *A. africanus* is compared with observed and

Table 2 Maternal-fetal weight relationships in pongids and hominids (from Leutenegger 1972*b*)

Species	Observed mean maternal weights		Observed mean fetal weights		Expected mean fetal weights	
	g	log	g	log	g	log
<i>Pongo pygmaeus</i>	37,000	4.56	1500	3.17	1550	3.19 ± 0.18*
<i>Pan troglodytes</i>	40,600	4.60	1600	3.20	1660	3.22 ± 0.19
<i>Gorilla gorilla</i>	90,000	4.95	2000	3.30	2890	3.46 ± 0.23
<i>Homo sapiens</i>	60,000	4.77	3300	3.51	2200	3.34 ± 0.21
<i>Australopithecus africanus</i>	22,500†	4.36			1120	3.05 ± 0.17

* 95% confidence limits.

† Estimate.

expected mean birth weights of pongids and modern Man. It is interesting to note that whereas expected values of fetal weights in the orang-utan and chimpanzee are almost identical to the observed values, in the gorilla the expected value overestimates the observed value, and in modern Man the expected value underestimates the observed value. In either species, however, the observed values fall within the 95% confidence interval of the expected values; this is also true for all other Primates investigated. For *A. africanus*, the estimated mean fetal weight equals log 3.05 with a 95% confidence interval from log 2.88 to log 3.22, which is numerically 1120 g with a range of 760 to 1660 g.

It already has been mentioned that with respect to birth weight modern Man has a unique position among living Primates. Viewing hominid evolution, how can this trend toward increased birth weight be interpreted? A possible answer can be obtained by using the similarity between maternal-fetal size relationship and brain-body size relationship, both representing negative allometric functions. With regard to brain-body size relationship in hominids, Kinzey (1972) and Leutenegger (1973a) have suggested that the increase in hominid cranial capacity during the Pleistocene has to be viewed as the result of a single allometric shift in the relationship between brain size and body size. Assuming that a similar trend, based on a single allometric shift, has affected the maternal-fetal weight relationship in *A. africanus*, the following inferences can be made. Birth weight of *A. africanus* would have to be estimated to be in the upper half of the expected range, between 1120 and 1660 g, and probably closer to the upper limit. Taking for example the exact upper limit (1660 g), the hominid regression line constituted by *A. africanus* and *Homo sapiens* would be perfectly parallel to the Primate regression line, maintaining the same constant of allometry (0.70), but differing from the latter by an initial size constant value of $\log b = 0.17$ which is numerically 1.47. A birth-weight estimate for *A. africanus* higher than 1660 g can be ruled out, since this would imply that in the hominid regression the constant of allometry would be lower than in the Primate regression. Even with this maximum possible estimate of birth weight, newborn *A. africanus* would still have been quite small, only slightly larger than average newborn chimpanzees and markedly smaller than average newborn gorillas.

Based on the birth weight estimate, head size of newborn *A. africanus* can be estimated as follows: newborn cranial capacity in relation to birth weight is quite constant among pongids and modern Man. As shown before, in chimpanzees relative cranial capacity of newborns averages 9.7%; in modern Man, the corresponding figure is 9.9%. Based on a relative cranial capacity of 9.8% and a birth weight estimate of 1120 g, newborn cranial capacity in *A. africanus* would be 110 cc. Based on the maximum birth weight estimate (1660 g), the corresponding cranial capacity would be 163 cc. The reasonableness of these figures can be tested by comparing them with the average cranial capacity of adult *A. africanus*, which has been calculated by Holloway (1970) to be 442 cc. Newborn *A. africanus* would thus have reached between 24.9 and 36.9% of the adult cranial capacity which compares excellently with the values for modern Man (23.3%; Todd, 1933) and chimpanzee (40.5%; based on data from Schultz 1940, 1941). Comparing the possible range of cranial capacity in newborn *A. africanus* (110–163 cc) with the actual range in newborn chimpanzees (139–171 cc; mean 155 cc), it can be inferred that the main dimensions of the head would have been very similar in these two forms. Mean head diameters for newborn chimpanzees are 83 mm (head length) and 71 mm (head breadth), respectively (Table 1). Since head dimensions of newborn *A. africanus* would have been only slightly different from those of newborn chimpanzees, they would

definitely have been smaller than the corresponding diameters of the pelvic inlet of STS 14. Even a newborn *A. africanus* with a head the size of a newborn gorilla (mean head length 97 mm; mean head breadth 79 mm) could have passed through the pelvic inlet of STS 14.

From these calculations it can be inferred that newborns of *A. africanus*, both in their body size and cranial dimensions were quite small in relation to the female pelvic inlet, these relationships being absolutely different from those in modern Man. Furthermore, these findings suggest that delivery in *A. africanus* was quick and easy which could have been a large selective advantage in a precarious environment.

3. Sexual Dimorphism

Since maternal-fetal size relationships, as demonstrated, differ markedly interspecifically, it can be inferred that selective pressure for the enlargement of the female pelvic inlet to ensure parturition must also vary interspecifically. As a consequence of interspecific differences in selective pressure for enlargement of the female pelvic inlet, interspecific differences in the degree of sexual differentiation in the pelvis have to be expected too.

Interspecific differences in the degree of sexual differentiation in the Primate pelvis have been reported in a number of papers (cf. van den Broek, 1911; Washburn, 1942; Schultz, 1949; Wettstein, 1963; Leutenegger, 1970*c*, 1973*b*; Black, 1970; Gingerich, 1972).

Sexual dimorphism in the pelvis is, however, not only influenced by maternal-fetal-size relationships but may also be an integral part of general secondary sexual differentiation (Schultz, 1949; Leutenegger, 1970*c*). In fact, general secondary sexual differentiation, which also varies markedly interspecifically (Schultz, 1956), may be as marked as to conceal sexual dimorphism in the pelvis resulting from the enlargement of the female pelvic inlet as a necessary requirement for the successful passage of the newborn. These two factors influencing the degree of pelvic sexual dimorphism are, however, separable (Leutenegger, 1970*c*).

Since the pubis constitutes part of the birth canal, whereas the ischium does not, and since the ischium is highly correlated with body size (Leutenegger, 1970*a*) sexual dimorphism in the ischio-pubic index primarily reflects the relative enlargement of the female pelvic inlet, while at the same time the index is independent on general secondary sexual differentiation. In all simian Primates studied so far, the means for the ischio-pubic index are higher in females than in males (Table 3). The degree of sexual dimorphism in this index can be expressed as the female mean as a percentage of the male mean. The highest degrees of sexual dimorphism in the ischio-pubic index are found in the squirrel monkey and the capuchin monkey, in both of which newborn cranial dimensions are largest compared to female pelvic dimensions. On the other hand, only slightly developed sexual dimorphism in the ischio-pubic index exists in the howler monkey and the pongids, in all of which newborn cranial dimensions are strikingly smaller than female pelvic dimensions.

Since the length of the pubis contributes to the transversal diameter of the pelvic rather than to the sagittal diameter, a correlation between degree of sexual dimorphism in the ischio-pubic index and the ratio between newborn's head breadth and transversal diameter of the female pelvic inlet can be postulated. In Figure 2, degrees of sexual dimorphism in the ischio-pubic index (based on data from Table 3) are plotted against

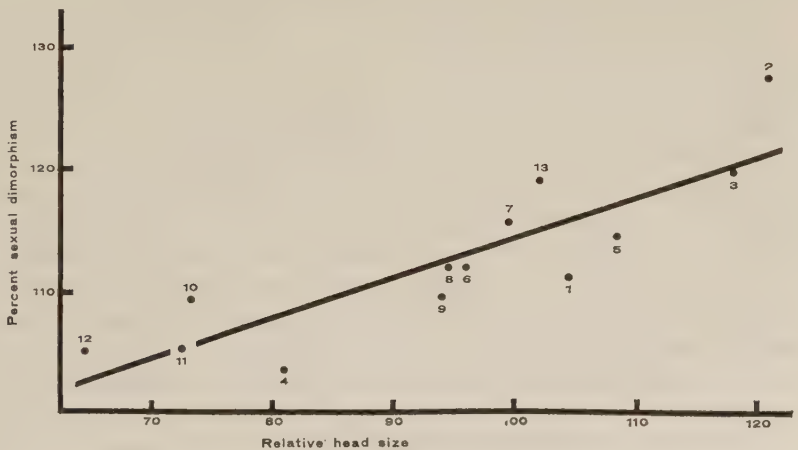
Table 3

Sexual differences and percentage sexual dimorphism for mean ischio-pubic index in simian Primates. (Data based on Schultz, 1949, and Leutenegger, 1970c)

Species	Ischio-pubic index			Per cent sexual dimorphism*
	Male mean	Female mean	Difference	
<i>Callithrix jacchus</i>	84.7	93.9	9.2	110.9
<i>Saguinus tamarin</i>	76.7	84.9	8.2	110.7
<i>Aotes trivirgatus</i>	71.8	83.3	11.5	116.0
<i>Saimiri sciureus</i>	73.0	92.9	19.9	127.3
<i>Cebus capucinus</i>	75.8	90.8	15.0	119.8
<i>Alouatta villosa</i>	111.3	115.3	4.0	103.6
<i>Lagothrix lagothricha</i>	98.7	112.9	14.2	114.5
<i>Ateles geoffroyi</i>	89.9	100.8	10.9	112.3
<i>Macaca mulatta</i>	82.9	95.7	12.8	115.4
<i>Nasalis larvatus</i>	86.4	96.9	10.5	112.1
<i>Hylobates lar</i>	92.7	101.6	8.9	109.6
<i>Hylobates moloch</i>	95.0	108.1	13.1	113.7
<i>Pongo pygmaeus</i>	97.8	107.0	9.2	109.4
<i>Pan troglodytes</i>	82.6	87.0	4.4	105.3
<i>Gorilla gorilla</i>	93.6	98.3	4.7	105.0
<i>Homo sapiens</i>	79.9	95.0	15.1	118.9

* Female mean in % of male mean.

Figure 2. Relationship between relative head breadth in newborns (mean newborn head breadth in % of mean transversal diameter of female pelvic inlet) and degree of sex differentiation in the ischio-pubic index (female mean in % of male mean) in 13 species of simian Primates. Corresponding values (Tables 1 and 3) are plotted against each other, and the least regression is drawn. Numerical designation of species: 1 *Callithrix jacchus*, 2 *Saimiri sciureus*, 3 *Cebus capucinus*, 4 *Alouatta villosa*, 5 *Lagothrix lagothricha*, 6 *Ateles geoffroyi*, 7 *Macaca mulatta*, 8 *Nasalis larvatus*, 9 *Hylobates lar*, 10 *Pongo pygmaeus*, 11 *Pan troglodytes*, 12 *Gorilla gorilla*, 13 *Homo sapiens*.



the ratios between newborn's head breadth and transversal diameter of the female pelvic inlet (= relative head breadth; based on data from Table 1). The least squares equation is y (degree of sexual dimorphism) = $81.51 + 0.329x$ (relative head breadth). The correlation coefficient is 0.86. These data clearly indicate that in simian Primates the degree of sexual dimorphism in the ischio-pubic index is highly correlated with the relationship between newborn cranial dimensions and dimensions of the female pelvic inlet. The degree of sexual differentiation in the ischio-pubic index can therefore be regarded as a direct measure for the degree of selective pressure for the enlargement of the birth canal as exerted by the fetus' cranial dimensions on the dimensions of the female pelvic canal.

With respect to the question of a development of pelvic sexual dimorphism in *Australopithecus africanus*, it can be inferred by analogy from living Primates that because of the smallness of newborn *A. africanus* selective pressure for enlarging the pelvic canal to ensure parturition may have been minor or even absent. This would then suggest that sexual differentiation in the ischio-pubic index in *A. africanus* may also have been minor, and definitely less pronounced than in modern Man. Since, at present, there can only be speculations about the degree of sexual dimorphism in body size, nothing can be said about the influence of general secondary sexual differentiation on pelvic dimensions.

4. Locomotory Adaptations

One of the most important functional dimensions on the mammalian pelvis from a locomotory viewpoint is the distance between sacroiliac- and hip-joint (Kummer, 1959a,b). Since body weight (in quadrupeds part of the body weight) is transmitted through the sacroiliac-joint, and ground reaction is transmitted by the hindlimbs through the hip-joint, torques are produced at these joints which tend to tilt the pelvis in a ventral direction (for further detail, see Kummer, 1959a,b; Leutenegger, 1970a). Besides depending on the part of the body weight transmitted through the hindlimbs, the amount of torques at these joints is also dependent on the length of the lever arm between them. The length of the lever arm is the result of two components: (1) the absolute distance between sacroiliac- and hip-joint, and (2) the degree of inclination of the pelvis from the horizontal plane. The more tilted up the sacroiliac-joint is in relation to the hip-joint, the shorter is the lever arm between the two joints.

In Primates there exist differences in the distance between the two joints as well as differences in the relative position one to another (Leutenegger, 1970a,b; 1972a). The two factors act in a compensatory fashion to keep the lever arm as short as possible. By keeping them apart for analysis, however, differences in each of them can be more or less clearly related to differences in the mode of locomotion. An osteometric measure for the distance between sacroiliac- and hip-joint is the lower iliac length (see footnote, Table 4). The ratio between lower iliac length and ischium length (Table 4) can therefore be regarded as a measure for the relative distance between sacroiliac- and hip-joint.

In Primates which are primarily quadrupeds (callithricids, small cebids, cercopithecines), regardless of the degree of arboreality or terrestriality, the distance between sacroiliac- and hip-joint is short. This is evident in relation to trunk length (Leutenegger, 1970a) as well as in relation to ischium length (Table 4). Because of approximately equal length of fore- and hindlimbs, the pelvis is subjected to highest mechanical stresses when the animals are progressing quadrupedally on the ground or on horizontal branches.

Table 4

Mean and range of variation of the ratio between lower iliac length* and ischium length categorized by locomotory patterns in simian Primates. (Data, except for *Australopithecus africanus*, based on Leutenegger, 1970a)

Locomotor category	Species	n	Lower iliac length in % of ischium length	
			Mean	Range
Quadrupedalism	<i>Callithrix jacchus</i>	30	114.1	96.0-128.0
	<i>Saguinus</i> sp.	62	99.3	87.5-112.5
	<i>Aotes trivirgatus</i>	7	109.4	100.0-115.8
	<i>Callicebus moloch</i>	1	100.0	
	<i>Saimiri sciureus</i>	17	103.7	85.7-117.6
	<i>Cebus capucinus</i>	18	123.5	107.1-152.0
	<i>Pithecia monachus</i>	1	108.0	
	<i>Cercopithecus</i> sp.	15	103.2	80.0-123.1
	<i>Erythrocebus patas</i>	1	108.1	
	<i>Macaca mulatta</i>	20	108.7	95.6-134.2
	<i>Cercocebus</i> sp.	6	112.9	95.6-140.0
	<i>Papio</i> sp.	17	106.0	85.0-123.5
Old World semibrachiation	<i>Colobus</i> sp.	1	100.0	
	<i>Presbytis</i> sp.	6	122.0	102.5-142.8
	<i>Nasalis larvatus</i>	4	113.8	104.0-137.9
Modified brachiation	<i>Pongo pygmaeus</i>	7	129.7	120.9-135.5
	<i>Pan troglodytes</i>	25	129.0	102.5-144.2
	<i>Gorilla gorilla</i>	24	110.2	91.4-125.9
New World semibrachiation	<i>Alouatta villosa</i>	8	152.9	145.2-171.4
	<i>Lagothrix lagothricha</i>	6	153.6	148.6-167.9
	<i>Ateles geoffroyi</i>	12	144.6	127.5-164.9
	<i>Hylobates lar</i>	45	165.6	136.4-200.0
True brachiation	<i>Symphalangus syndactylus</i>	5	188.5	164.0-210.2
	<i>Homo sapiens</i>	21	77.7	62.5- 95.5
Bipedalism	<i>Australopithecus africanus</i>	1	95.6†	

* Lower iliac length (= Untere Iliumlänge, Leutenegger, 1970a), as an osteometric measure for the distance between sacroiliac- and hip-joint, equals the distance between the center of the acetabulum and the point of intersection between the arcuate line and the articular auricular surface.

† This value is based on an ischium length of 45 mm, and lower iliac length of 43 mm. The measurements were taken on a cast (Wenner-Gren Foundation) representing STS 14. The measurement for the ischium length coincides with that given by Robinson (1972). Measurements of the lower iliac length are not given in the literature.

The pronograde posture is reflected in a horizontal position of the pelvis which indicates that the length of the lever arm between sacroiliac- and hip-joint equals the absolute distance between the two joints. In these Primates, torques at the two joints are kept minimal by selective pressure for an absolute distance between the two joints as short as possible. The mechanical requirement to keep the distance between the two joints as short as possible is opposed, however, by the need for a sagittal diameter in the female pelvic large enough for a successful passage of the fetus' head. The opposing action of these selective forces probably exists in all quadrupedal Primates, but it is particularly evident in large-sized cercopithecines. For example, in adult female baboons there is the development of a promontorium in the lumbo-sacral region of the vertebral column only found in a similar degree in hominids (Schultz, 1961). In contrast to the condition in hominids, in whom the promontorium reflects the tilt-up of the presacral region as an

adaptation to erect posture, the dorsoflexion of the sacrum in female baboons causes an increase in the sagittal diameter of the pelvic canal, particularly its outlet, without however influencing disadvantageously the distance between sacroiliac- and hip-joint. Old World semibrachiators represented by the colobines follow the same pelvic construction as quadrupeds.

In the New World semibrachiators, (*Alouatta*, *Lagothrix*, *Ateles*, *Brachyteles*), and in the true brachiators (hylobatids) the distance between sacroiliac- and hip-joint is increased compared to the condition in quadrupeds. The elongation of this distance is evident in relation to trunk length (Leutenegger, 1970a) as well as in relation to the length of the ischium (Table 4). The increase in the distance between the two joints can be explained best by assuming that in these Primates selective pressures based on newborn cranial dimensions for expansion of the female pelvic canal are not as strongly opposed by selective forces to keep the distance between sacroiliac- and hip-joint minimal.

This theory can be supported by the following two facts. (1) Whereas quadrupedal Primates primarily progress in a pronograde posture, in New World semibrachiators and true brachiators, when progressing bipedally or by brachiation, the trunk is more often in a vertical posture. This causes a tilt-up of the pelvis which results in a shortening of the projective distance between sacroiliac- and hip-joint and consequently in a shortening of the lever arm between the two joints. It follows that reduction of the torques at the two joints can be gained without a decrease in the actual distance between the two joints, thus resulting in a decrease of selective pressure for a minimal distance between the two joints. (2) A comparison of cranial dimensions of newborns, whose mothers are of equal body size, reveals that newborns of primarily brachiating Primates have larger cranial dimensions than those of primarily quadrupedal Primates (Leutenegger, 1970a,b). As a consequence, to ensure successful passage of the fetus at term, pelvic inlet dimensions in brachiating Primates have to be larger than in quadrupedal Primates of equal body size. The increase of the distance between sacroiliac- and hip-joint in New World semibrachiators and true brachiators can therefore be interpreted as an adaptation for a newborn head size relatively larger than in quadrupeds, with simultaneous reduction of selective pressures for a minimal distance between the two joints as a result of a vertical rather than a pronograde posture. It even can be speculated that the expansion of the brain in the Atelinae compared to other cebids, and in the hylobatids compared to the cercopithecoids (Schultz, 1956) may be related to reduced selective pressures on the distance between sacroiliac- and hip-joint which result from a different mode of locomotion.

In pongids, categorized as modified brachiators (Napier & Napier, 1967), the distance between sacroiliac- and hip-joint is also elongated, compared to the condition in quadrupeds. The elongation is particularly obvious when set in relation to the trunk length (Leutenegger, 1970a). Less obvious is the elongation when related to ischium length (Table 4), because the ischium is elongated too, although not as much. Since in pongids female pelvic inlet dimensions are strikingly larger than corresponding newborn cranial dimensions, the increase in distance between sacroiliac- and hip-joint can at first sight hardly be regarded as a result of selective pressure for expansion of the birth canal to ensure parturition. It can be assumed, however, although there is no direct evidence, that at an early stage of pongid evolution, as this has been demonstrated for many other lineages, adult body size was much smaller than it is in extant pongids. Based on the analysis of maternal-fetal size relationships (Leutenegger, 1974) it

can be inferred that at least in the gorilla the large body size is a relatively recent phenomenon, which suggests that, in contrast to Pilbeam's (1970) view, Miocene ancestors of gorilla were much smaller in body size than modern gorilla. Since Primates of smaller body size have relatively larger newborns, this would then suggest that at an early stage in pongid evolution newborn cranial dimensions would have been larger in relation to female pelvic dimensions. This would have then resulted in selective pressure for expansion of the pelvic canal, including an increase in distance between sacroiliac- and hip-joint.

As a consequence of subequal length of fore- and hindlimbs, in pongids, when progressing quadrupedally, the trunk is sloping backward, affecting the position of the pelvis. The pelvis is more or less tilted up; the degree of inclination depending on intermembral length relationship and whether or not the hands are in knuckle-walking position. In any case, the inclination of the pelvis causes a reduction in the projective distance between sacroiliac- and hip-joint, which results in a shortening of the length of the lever arm between the two joints. This suggests that in pongids, similar to hylobatids and large cebids, selective pressure for reducing the actual distance between sacroiliac-joint and hip-joint might be reduced. If this holds true, the reduction of selective pressure would explain why no shortening of this distance occurred when the African pongids became to a high degree terrestrial quadrupeds.

In contrast to the non-hominid Primates, in which only part of the body weight is supported by the hindlimb, in hominids as a result of the habitual erect posture, the whole body weight has to be supported by the hindlimb. In hominids reduction of disadvantageous torques at the sacroiliac- and hip-joint has been brought about by the most fundamental structural change in the Primate pelvis: the rotation in dorso-caudal direction of the *Facies sacralis ossis ilii*, which comprises the iliac tuberosity and the auricular surface. This modification has caused a strong reduction of the distance between the sacroiliac- and hip-joint, and in upright posture has moved the sacroiliac-joint vertically above the hip-joint, thus minimizing the length of the lever arm between the two joints in a twofold manner. In *Homo sapiens* the reduction of the distance between the two joints is more marked than in any other living Primate. This is evident when the distance between the two joints is compared to trunk length (Leutenegger, 1970a) as well as compared ischium length (Table 4). As Washburn (1950) points out, however, selective forces for shortening of the distance between sacroiliac- and hip-joint is clearly opposed by selection for a pelvic canal large enough to guarantee successful passage of the newborn. The opposing action of these selective forces and their varying intensity in the two sexes is clearly reflected by the development of marked pelvic sexual dimorphism, not only in the ischio-pubic index, but also in the shape of the sciatic notch, the shape of the obturator foramen, the size of the subpubic angle, etc.

In *Australopithecus africanus*, the distance between the two joints is also highly reduced. This is particularly evident when compared to body size. Compared to skeletal trunk length (Biegert & Maurer, 1972) as a measure of body size in fossil Primates, in *A. africanus* the lower iliac length equals a value of 11%, which is almost identical with the mean value (10.5%) of *Homo sapiens*. Compared to ischium length, lower iliac length in *A. africanus* seems not to be as strongly reduced as in modern Man (Table 4). Taking into account, however, that the ischium is extremely short in *A. africanus* (Robinson *et al.*, 1972), reduction of the lower iliac length only appears to be less marked than in modern Man. It therefore can be inferred that regarding construction of the hominid pelvis, at

least where the distance between sacroiliac- and hip-joint is concerned, *A. africanus* was as advanced as modern Man. This interpretation is strongly supported by the findings on the relationship between newborn cranial dimensions and the dimensions of the female pelvic inlet. The estimate that in *A. africanus* newborn cranial dimensions have been significantly smaller than corresponding dimensions of the female pelvic inlet suggests that prior and during the australopithecine stage of hominid evolution selective pressure for enlarging the pelvic canal to ensure parturition may have been minor or even absent. As a consequence, selective forces toward highly efficient construction of the pelvis for bipedalism could have acted more strongly. This model of interaction of selective forces resulting from both locomotory and obstetrical functions provides the basis for Robinson's (1971) hypothesis that *A. africanus* was at least as well adapted to bipedal locomotion as modern Man.

5. Summary and Conclusions

In analyses of Primate pelvic morphology from a functional viewpoint, traditionally only selective forces resulting from locomotory functions have been taken into account. This paper recognizes the significance of selective forces resulting from obstetrical functions, without consideration of which a functional analysis of the pelvis can only be fragmentary.

It is demonstrated that the degree of selective pressure for enlargement of the female pelvic canal to ensure successful delivery is mainly dependent on the relationships between cranial dimensions of the fetus at term and corresponding dimensions of the female pelvic inlet. These relationships are dependent on two main factors: (1) size of the fetus at term relative to the size of the mother, and (2) degree of encephalization at birth. Since maternal-fetal size relationships as well as newborn brain-body size relationships represent negative allometric functions, the addition of these two components results in newborn cranial dimensions of small-sized Primates generally much larger relative to maternal size than in larger-sized Primates. It follows that, as a general rule (exceptions in the text), in smaller-sized Primates there is a higher degree of selective pressure for enlargement of the birth canal than in larger-sized Primates.

The selective forces resulting from obstetrical functions are, however, opposed to a varying degree by selective forces resulting from locomotory functions, the degree of which depends on the mode of locomotion. In quadrupeds (including Old World semibrachiators) and particularly bipeds, there is strong selective pressure to minimize the distance between sacroiliac- and hip-joint, while in modified brachiators, New World semibrachiators, and true brachiators the selective pressure is reduced to varying degrees.

Since selective forces resulting from obstetrical functions as well as those resulting from locomotory functions vary interspecifically, their interaction also varies interspecifically. Pelvic morphology in Primates reflects an adaptational complex determined by at least 3 different components: mode of locomotion, maternal-fetal size relationship, and degree of encephalization at birth.

Based on the analysis of these components in living Primates, an estimate of their degree and interaction in *Australopithecus africanus* can be given, which should help to further elucidate the problem of the evolution of hominid bipedalism. The evidence suggests that newborns of *A. africanus* were quite small in relation to the female pelvic inlet which would indicate that (1) delivery in *A. africanus* was quick and easy which could have been a large selective advantage, and that (2) in the early stages of hominid

evolution selective pressures for enlarging the pelvic canal may have been minor or even absent; selective forces toward highly efficient construction of the pelvis for bipedalism could have been stronger which would support the hypothesis that *A. africanus* was at least as well adapted to bipedal locomotion as modern Man.

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Laura Newell Morris
Barbara A. Kerr

*Regional Primate Research Center
and Department of Anthropology,
University of Washington, Seattle,
Washington 98195, U.S.A.*

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Genetic Variability in Macaques: Correlations Between Biochemical and Dermatoglyphic Systems

The palmar dermatoglyphics of four groups of macaque, *Macaca nemestrina*, *M. fuscata yakui*, *M. f. fuscata* and *M. fascicularis*, were compared, and the genetic affinities of the four groups were assessed using a dermatoglyphic mean square distance measure. According to this measure the two subspecies of *M. fuscata* were dermatoglyphically more distant from one another than was *M. fuscata fuscata* from *M. nemestrina*, suggesting that the two insular populations of *M. fuscata* had evolved in genetic isolation. The distributions of specific dermatoglyphic patterns were then compared with the frequency distributions of alleles at different protein structural loci in other macaque populations. The results of the comparison were consistent in that insular populations showed reduction in variability for both kinds of systems. The implications of this correlation are discussed in terms of population size and natural selection.

1. Introduction

Dermatoglyphic analysis is a useful tool for comparing phenotypes among human populations (see review by Biswas, 1961). In fact, it has been suggested that dermatoglyphics may convey more information concerning population relationships than do simple genetic traits (Rife, 1954; Roberts *et al.*, 1968); at least, data from the two sources appear to be mutually complementary in human populations studied (Birdsell, 1952; Newman, 1960).

Non-human Primates also possess digital, palmar and plantar dermatoglyphic patterns which can be described by standard dermatoglyphic nomenclature (Wilder, 1902; Whipple, 1904; Midlo & Cummins, 1942; Cummins & Midlo, 1943; Biegert, 1961). Some dermatoglyphic studies have been conducted for species or population analyses (Furuya, 1962; Iwamoto, 1964, 1967; Brehme, 1964, 1965, 1967_{a,b} 1968_{a,b,c}). Such studies are valuable because they (1) provide information on the amount of phenotypic variability present within and among any given population(s), and (2) permit comparison of the degree of inter- and intra-population dermatoglyphic variability with that described for various Primate populations with respect to Mendelian biochemical traits.

The present study compares four groups of *Macaca* using dermatoglyphic analyses, and discusses the results with reference to data available for various structural protein genetic loci.

2. Sample and Methods

The four macaque groups used for dermatoglyphic comparisons are listed in Table 1. Only groups with sample numbers large enough to permit good comparison were used. Groups were compared on the basis of pattern types, palmar pattern intensities, and a biological distance measure.

Hand prints of *M. nemestrina* were obtained by the method of Tips, Shining and Perkins (1964) (Plate 1). Palm prints of the other species referred to here were obtained by standard inking procedures. The palmar configurational areas and the pattern types that were analyzed are illustrated in Plate 1; these are the basis of the percentage distributions given in Table 2. To obtain the percentages, data from the right and left

Table 1

Macaca groups used for dermatoglyphic comparisons

Group	Geographic origin	Number*
<i>M. nemestrina</i> (Kerr & Morris, in preparation)	Malaysia	79
<i>M. fuscata yakui</i> (Iwamoto, 1964)	Japan (Yakushima, Kagoshima)	42
<i>M. fuscata fuscata</i> (Iwamoto, 1964)	Japan (Takasakiyama, Orta)	56
<i>M. fascicularis</i> † (Furuya, 1962)	S. E. Asia	112

* Number of animals refers to the maximum number used. The actual number of palms analysed varies among configurational areas in the studies of Iwamoto and Furuya (see Table 2).

† Referred to by Furuya as *Cynamolgus irus*.

hands of both sexes were combined. From these percentages the mean configurational area and total pattern intensities were calculated according to the method of Midlo & Cummins (1942). Each pattern type was rated on a scale of increasing complexity of 0 (open field) to 1.0 (whorl and double loop), and from the pattern type percentages, the mean pattern intensity for each configurational area was obtained. The seven individual areal values were then summed to give a total pattern intensity value for the sample in question.

From the same pattern percentages a biological distance measure called mean square distance was calculated. The measure, referred to by Hughes (1967) as "dermatoglyphic distance," provides a means of quantitatively assessing affinities and distances between the macaque groups. Other more elaborate distance measurement statistics exist, but Hughes, after applying these to his human dermatoglyphic data, concluded that the dermatoglyphic distance measure provided as much information as did any other measurements of population affinities.

Determining dermatoglyphic distance involves setting a particular group as a point of origin and calculating the dermatoglyphic pattern frequency differences between it and each sample with which it is to be compared. The differences are then squared to remove negative signs, and the mean of the squared distances (M.S.D.) is calculated for each intra-pair comparison. These computations measure the "dermatoglyphic intra-pair distance" between only the origin sample and any other group. The computation must be redone for each different sample, using it as the point of origin for other estimates of dermatoglyphic distance.

The method has thus far been applied only to digital pattern frequencies in human populations (Hughes, 1967; Roberts *et al.*, 1968). Here we use the frequencies of the different pattern types found in the seven configurational areas (see Table 2). A mean square distance was obtained for each configurational area and the area values were averaged to give a total mean square distance for each intra-pair group comparison (Table 3).

The results of the dermatoglyphic analyses are discussed with reference to biochemical variation within and between groups of *Macaca*. The geographic distribution of these groups is illustrated in Figure 1.

Plate 1. A. Photograph of plastic palmar mold and schematic representation of configurational areas in *Macaca* palm. B. Pattern types: O, open field; L, Loop; D, double loop; W, whorl.

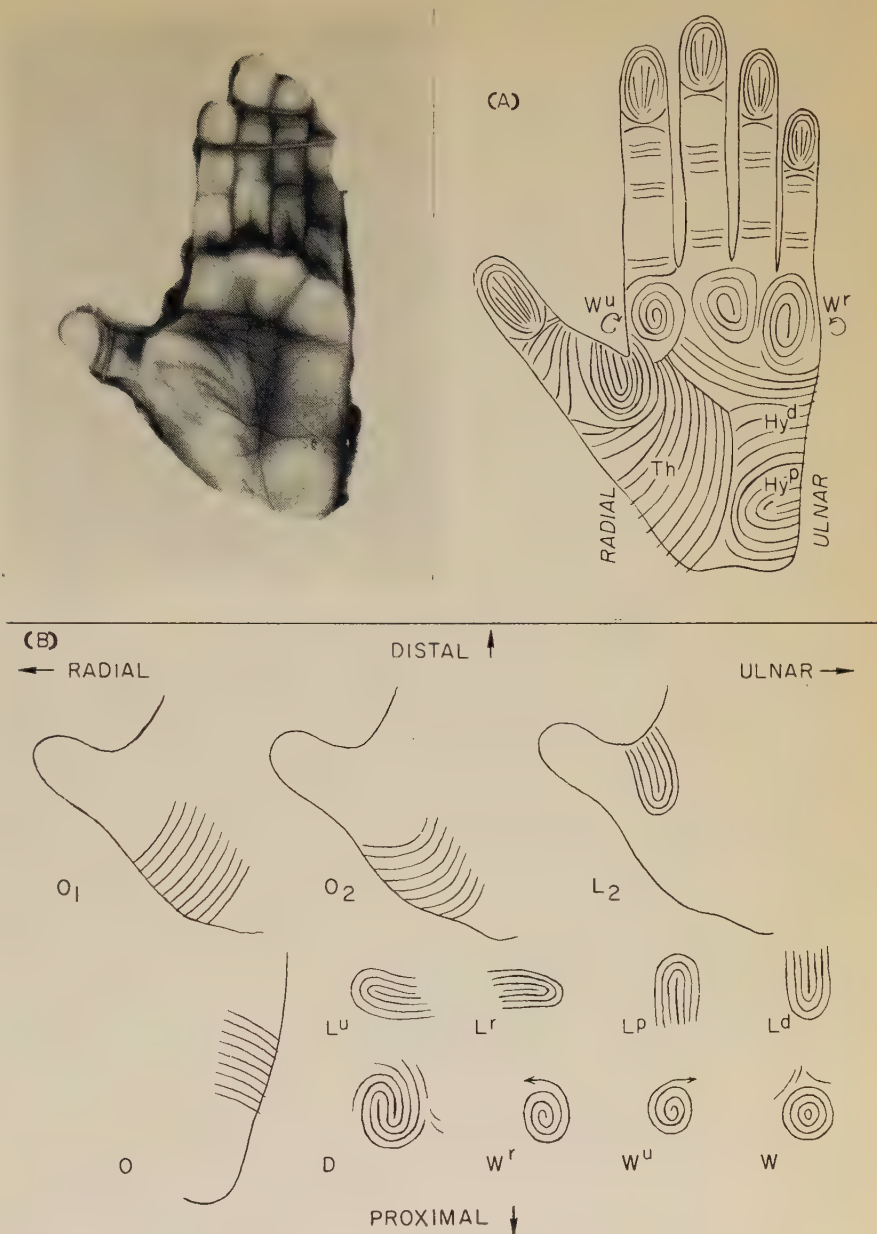




Table 2

Palmar patterns in four groups of *Macaca**

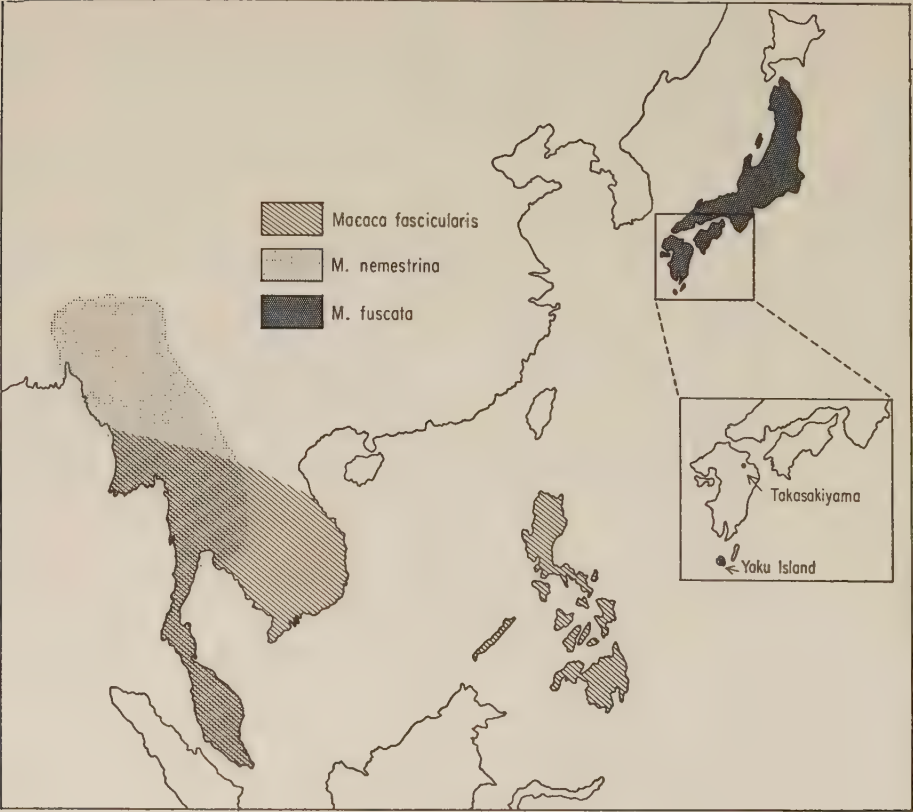
Sample	Thenar					Hypothenar ^p					Hypothenar ^d						
	No. hands	O ¹	O ²	L ¹	L ²	No. hands	V	L	D	W	No. hands	O	V	L ^r	L ^u	(L)	W
<i>M. fuscata yakui</i>	83	0	16.9	8.4	74.7	84	0	85.7	14.3	0	84	100	0	0	0	(0)	0
<i>M. fuscata fuscata</i>	111	66.7	0	33.3	0	111	0	27.9	49.5	22.5	112	68.8	0	10.7	17.9	(28.6)	2.7
<i>M. nemestrina</i>	157	47.8	46.5	0	5.7	157	0	81.5	17.2	1.3	157	93.6	0	0.6	4.5	(6.5)	0
<i>M. fascicularis</i>	—	—	—	—	—	224	1.8	33.0	41.5	22.3	224	53.1	11.2	—	—	(26.8)	7.6

* Only the main types of patterns in the seven configurational areas which are recorded for all groups are included here. Therefore, in some cases the area percent may not total 100. Parentheses indicate combined values.

Table 3 **Mean square distance (M.S.D.) of configurational areas in four groups of *Macaca***

Group	Th	Hy ^b	Hy ^a	I	II	III	IV	Total M.S.D.
M.S.D. from (a)								
(a) <i>M. nemestrina</i>								
(b) <i>M. fuscata yakui</i>	5990.8	9.2	22.2	522.2	732.0	15.4	345.8	1091.0
(c) <i>M. fuscata fuscata</i>	761.8	1456.6	392.3	943.0	694.0	251.3	364.2	638.7
(d) <i>M. fascicularis</i>	—	1128.9	722.8	296.2	595.0	112.3	254.4	518.3
M.S.D. from (b)								
(b) <i>M. fuscata yakui</i>								
(c) <i>M. fuscata fuscata</i>	2480.0	1695.4	601.6	80.6	0.54	142.7	0.71	714.5
(d) <i>M. fascicularis</i>	—	2758.8	99.2	1275.3	9.6	54.5	10.1	701.2
M.S.D. from (c)								
(c) <i>M. fuscata fuscata</i>								
(d) <i>M. fascicularis</i>	—	30.0	90.2	1688.3	6.7	49.3	12.1	312.8

Figure 1. Asian distribution of macaque species from which dermatoglyphic and biochemical data were drawn. The *M. nemestrina* sample studied in the dermatoglyphic comparisons and referred to by Gerald *et al.* (1970) in the biochemical comparison (Table 4) included many of the same animals and originated in the southern sector of Malaysia.



3. Results

The percentage distributions of the major palmar patterns are summarized in Table 2. If only major pattern types (open, loop, double loop and whorl) are considered, certain generalizations may be made about the seven configurational areas. Interdigitals II, III and IV are the least variable among groups. They show a high percentage of whorls (70 to 100%), although a group may drop to a middle value (about 65%) in one area or another. In this respect, *M. nemestrina* showed the lowest total percentage of whorls (interdigitals II and IV, 63.8 and 68.8%, respectively). However, if pattern complexity, rather than pattern type alone, is considered, and double loops (D) are included with whorls, all groups attain combined percentages of over 80% with the exception of interdigital II in *M. nemestrina* (71.4%).

Interdigital I shows fairly consistent percentages for the presence of loops among all groups (25 to 45%). Whorls drop to low values (about 10%) in the two *M. fuscata* subspecies, but again inclusion of double loops brings all four groups to intermediate combined values of about 55 to 70%.

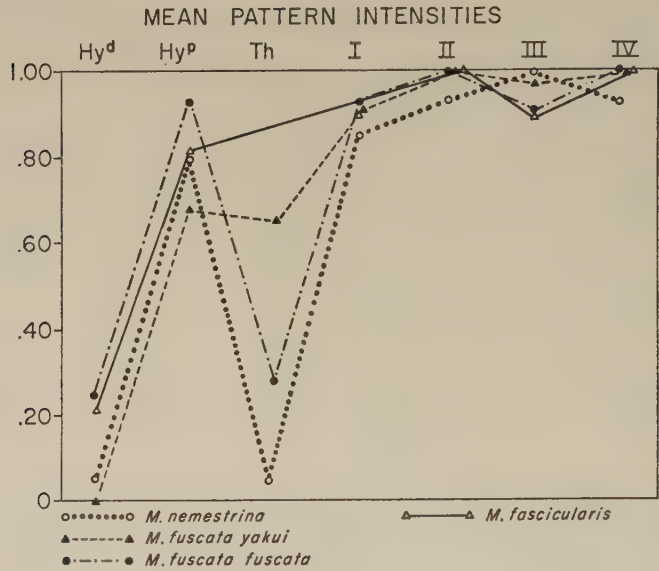
Thus, in the above four areas the four groups present a somewhat consistent macaque patterning. In the remaining three areas, however, the patterning is more variable. In the thenar area, although only two major patterns (open fields and loops) are observed, the frequency of occurrence seems to be distributed randomly among the groups. The percentage of open fields is high in *M. nemestrina* (94.3), intermediate in *M. f. fuscata* (66.7), and low in *M. f. yakui* (16.9). In the hypothenar proximal area the percentage of whorls is low, but the range is wide (0–22.5%). This range is further increased if complexity is admitted by the inclusion of double loops, becoming 14.3 to 72.0%. The range of loop percentages is also wide (27.9 to 85.7). In the hypothenar distal area open fields are the most frequent pattern type, but again with a wide range of distribution (53.1 to 100%).

Regarding these three most variable palmar areas, it is noteworthy that the two subspecies, *M. f. yakui* and *M. f. fuscata*, are as different from one another as are the separate species, *M. nemestrina* and *M. fascicularis*. This differential persists when the major pattern types are reduced to subtypes based on pattern direction. Although in the interdigital areas there are definite intergroup differences between the *M. fuscata* subspecies with respect to actual percentages of pattern subtypes, a general trend prevails. For example, if the radial whorl is the most frequent subtype in *M. f. yakui*, it is also the most frequent subtype in *M. f. fuscata*, although the actual percentages differ. However, in the thenar area 0^2 is the most frequent subtype pattern in *M. f. yakui*, while 0^1 is the most frequent subtype in *M. f. fuscata*.

As Midlo & Cummins (1942) have shown, such tabulated percentages of dermatoglyphic patterns are not well adapted to the tracing of affinities and differences among taxa nor among separate configurational areas, making it difficult and confusing to summarize all the data in any meaningful way. Therefore, the configurational area percentages were converted into pattern intensity values (Fig. 3). The total pattern intensities were 5.37 (*M. f. yakui*), 5.29 (*M. f. fuscata*), 4.60 (*M. nemestrina*), and 4.82 (*M. fascicularis*).

The differences in the total values derive primarily from the wide range of intensity values characterizing the two most variable areas, i.e. the thenar and hypothenar distal. Interestingly, the group differences observed in the pattern percentages for the hypothenar

Figure 2. Configurational area pattern intensities in four groups of macaque.

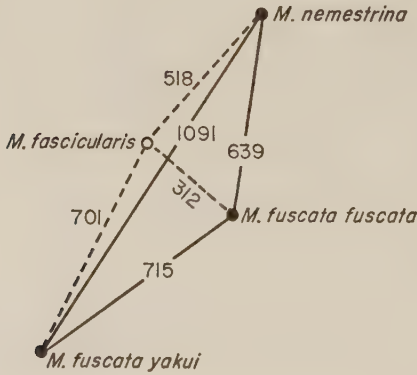


proximal area are obscured when converted to pattern intensity values. The range of thenar values, from 0.05 (*M. nemestrina*) to 0.67 (*M. f. yakui*), is the widest of all configurational areas. The values for the hypothenar distal area are the lowest of all areas, and also show a wide range (0 to 0.25).

The hypothenar proximal area exhibits significantly higher pattern intensity values and a smaller inter-group range (0.80 to 0.93) than do the thenar and hypothenar distal areas. The four interdigital areas consistently show the highest values of all palmar areas among the four macaque groups. In some areas the value is 1.0 or close to it, i.e. 0.99. These values reflect the high percentages of whorls and double loops already described.

Figure 3. Total mean square distances among the four groups of macaque.

TOTAL DERMATOGLYPHIC M.S.D



Again, the intensity values show the same situation as did the pattern frequencies; in the two most variable areas the two subspecies are as different from one another as are the separate species (Figure 3). Thus, both the pattern percentages and pattern intensity values give an indication of the dermatoglyphic similarities and dissimilarities among the macaque groups. However, we believe that the measure called "dermatoglyphic distance," as suggested by Hughes (1967), provides a better quantitative assessment of affinities and distances among our macaque groups (Table 3).

In interpreting the results, it should be remembered that whereas dissimilarity of dermatoglyphic distances between two populations probably indicates genetic dissimilarity, similarity may or may not reflect close genetic affinity. Total mean square distance value (Table 4) shows *M. nemestrina* furthest from *M. f. yakui* (M.S.D. 1091.0). Interestingly, the next furthest distant populations are the two subspecies of *M. fuscata* who show greater dissimilarity from one another (M.S.D. 714.5) than either does from *M. fascicularis* or than *M. f. fuscata* does from *M. nemestrina* (Table 3).

Comparing mean square distances (Table 3) with pattern intensities (Figure 2) reveals that the two sets of values are generally consistent. For example, in the highly variable thenar area the different intensity value of 0.67 (*M. f. yakui*) vs. 0.05 (*M. nemestrina*) is paralleled in the highest area mean squared distance of 5990.8 between the two groups. However, mean square distance is a more sensitive measure of absolute intergroup pattern differences which may be obscured by the method used to calculate mean pattern intensity.

4. Discussion

Several studies using biochemical data have evaluated genetic variability in macaques (see Table 4). For many of the biochemical variants observed monogenetic control is postulated with little or no environmental influence. Palmar dermatoglyphic patterns, on the other hand, are the product of a polygenic system differentially influenced by the environment (Loesch, 1971). As such, they present a phenotypic system that might prove useful in adding supplementary data to inter- and intra-species comparisons of macaques using Mendelian biochemical traits.

It is impossible to compare our dermatoglyphic distance measurements with most of the macaque population distances (dissimilarity indices) based on biochemical data (Prychodko & Goodman, 1971; Weiss & Goodman, 1971a). Although the investigators include groups of the same species as our populations, their groups are not identified well enough geographically to allow accurate comparisons of their dissimilarity indices with our dermatoglyphic distance measures. However, one paper contains dissimilarity indices on comparable macaque populations. Prychodko & Goodman (1971) using phenotypic frequencies of five biochemical systems calculated indices of dissimilarity which show *M. fuscata* with a greater affinity to *M. nemestrina* from Thailand and Malaysia (indices ~ 0.52) than to *M. fascicularis* from the Philippines and Malaysia (indices ~ 0.69). These results are consistent with our mean square distance measure showing *M. f. yakui* closer to *M. nemestrina* (M.S.D. = 1091.0) than to *M. fascicularis* (701.2). However, distance measures of *M. f. fuscata* show this group closer to *M. fascicularis* (M.S.D. = 312.8) than to *M. nemestrina* (M.S.D. 638.7). However, if dermatoglyphic data from the two *M. fuscata* groups are combined into the "species" *M. fuscata*, the mean square distance measures then give the same relationships to *M. nemestrina* and *M. fascicularis* as do the biochemical

Table 4 Number of alleles present at polymorphic frequencies ≥ 0.01

Biochemical variants	Insular				Mainland				
	<i>M. fuscata yakui</i>	<i>M. fuscata fuscata</i>	<i>M. fascicularis</i> (Phil.)	<i>M. fascicularis</i> (Thailand)	<i>M. fascicularis</i> (Malaysia)	<i>M. fascicularis</i> (Cambodia)	<i>M. nemestrina</i> (Thailand)	<i>M. nemestrina</i> (Malaysia)	
Transferrin (Lai, 1972)	—	—	1 (116)	8 (77)	7 (179) 7 (137)	—	5 (137)	—	
(Prychodko <i>et al.</i> , 1969)	2 (197)	—	—	—	—	—	—	—	
(Ishimoto, Toyomasu & Uemura, 1967)	1 (130)	—	—	—	—	—	—	—	
Carbonic anhydrase I (CAI) (Tashian <i>et al.</i> , 1971)	1 (17) 1 (17)	2 (103) 1 (76)	1 (74) 2 (16)	2 (136) 2 (17)	2 (261) 2 (49)	—	3 (46)** 2 (17)	3 (111)** 2 (12)	
Carbonic anhydrase II (Tashian <i>et al.</i> , 1971)	—	—	—	—	—	—	—	—	
Prealbumin (Weiss & Goodman, 1971b)	1 (55)	—	2 (58)	1 (119)*	2 (211)	—	2 (36)*	1 (111)	
6-PGD (Gerald <i>et al.</i> , 1970)	—	—	1 (78)	2 (136)	3 (263)	—	1 (63)	2 (243) 2 (162)	
(Prychodko <i>et al.</i> , 1971)	1 (147)	—	—	—	—	—	—	—	
Esterase AI (Weiss & Goodman, 1972)	—	—	2 (58)	1 (119)*	1 (76)	—	—	—	
$\alpha 1$ -antitrypsin (Omoto, Tanaka & Prychodko, 1970)	2 (37)	3 (151)	3 (54)	3 (111)	3 (223)	—	3 (64)	3† (151)	

(Gerald *et al.*, 1970)
(Ishimoto & Kuwata, 1972)
NADH Diaphorase
(Ishimoto, 1971)

$$\begin{array}{cccc} \text{Hy}^p & \text{Hy}^d & \text{II} & \text{IV} \\ \left\{ \begin{array}{c} \text{L} \\ \text{D} \end{array} \right\}_W & \left\{ \begin{array}{c} \text{O} \\ \text{L} \end{array} \right\}_W & \left\{ \begin{array}{c} \text{L} \\ \text{D} \end{array} \right\}_W & \left\{ \begin{array}{c} \text{L} \\ \text{D} \end{array} \right\}_W \end{array}$$

† Includes one allele of 0.0099 frequency.
‡ Animals from Takasakyama.
** All animals of CAI phenotype were excluded as it is not known if this phenotype is the result of allelic variation at the CAI locus or repression mediated by action at another locus.

×	+	0
Fixation ≥ 0.99 .	Present.	Absent.

dissimilarity indices. These distance measures serve to emphasize the importance of considering the component geographic populations of a total species, especially when the latter are insular populations, as are the *M. fuscata*.

As set forth above, the insular Japanese subspecies *M. f. fuscata* is geographically and taxonomically closer to the insular subspecies *M. f. yakui* than it is to the species *M. nemestrina*; nevertheless, *M. f. fuscata* has greater distance from *M. f. yakui* (M.S.D. 714.5) than it has from *M. nemestrina* (M.S.D. 638.7). Moreover, *M. f. yakui* shows the greatest total intra-pair distances when compared with each of the other three macaque groups. A comparable situation has been reported by Prychodko *et al.* (1969) who used transferrin frequencies to construct an index of population dissimilarity. They show that the intra-species differences between *M. fascicularis* from Thailand and the insular *M. fascicularis* from the Philippines were as great (dissimilarity index 0.552) as the interspecies differences between *M. nemestrina* and *M. fascicularis*, both from Thailand (dissimilarity index 0.526).

One conclusion to be drawn from the above facts is that the results of the dermatoglyphic comparisons based on the *M. fascicularis* sample should be very broadly interpreted. We were unable to ascertain the geographic origin of the *M. fascicularis* included in Furuya's (1962) sample, and we would predict, for example, that inclusion or exclusion of Philippine *M. fascicularis* would significantly affect the total dermatoglyphic pattern frequencies. The biochemical data suggest that the result of combining two *M. fascicularis* dermatoglyphic samples, one insular and one mainland, might be similar to the result described when dermatoglyphic frequencies from the two subspecies of *M. fuscata* were combined, i.e. a series of mean frequencies which obscure the often large phenotypic and genotypic differences between intraspecific groups.

When the results of our dermatoglyphic comparisons are examined in relation to the gene frequency distribution of biochemical variants, a consistent trend emerges: insular populations of macaques show less phenotypic and gene pool variability. Both subspecies of *M. fuscata* show a loss of variability in the range of pattern types expressed in some palmar configurational areas (Table 4). *M. f. yakui* has reached fixation of a single pattern (≥ 0.99) in four of the seven configurational areas (Hy^p , loops; Hy^d , open pattern; interdigitals II and IV, whorls). Like *M. f. yakui*, *M. f. fuscata* has also reached fixation of the whorl pattern in interdigitals II and IV. This loss of phenotypic dermatoglyphic variability in the two insular macaque groups is compared in Table 4 with the loss of variability recorded by investigators in various biochemical systems of insular macaques. In dermatoglyphic patterns, *M. f. yakui* has lost more variability (four areas fixed) than *M. f. fuscata* (two areas fixed). The biochemical data are consistent with the dermatoglyphic results in that *M. f. yakui* shows a reduced number of alleles for three out of four biochemical traits when compared with *M. f. fuscata* (Table 4).

The paramount question of why insular or marginal populations lose variability has been fully discussed by Weiss & Goodman (1971*a,b*), following the explanation of Mayr (1954) and of Dobzhansky & Pavlovsky (1957). In brief, they propose that small populations, when initially isolated, contain an uneven representation of allelic variation at multiple loci through sampling error (founder effect). The original sampling error may disrupt the previously co-adapted character of the total genome. Thus, an allele which was selectively established in a gene pool because of its functional ability in a wide range of genetic backgrounds may, in the more genetically limited insular situation, become disadvantageous to the small population. Such a sudden modification of the genetic

environment, affecting as it does the selective values at all loci simultaneously, initiates a massive genetic shock to the population. The initial reduction in genetic variability through genetic drift will be followed by a further reduction due to selection, with drift and selection interacting to establish a new co-adapted gene pool within which variability will eventually increase. (For a discussion of the interaction of drift and selection in small populations, see Wright, 1951.)

Certainly, the Japanese subspecies of *M. fuscata*, especially *M. f. yakui* of Yakushima Island, currently exist in geographic situations ideal for the past genetic divergence of previously contingent, very similar macaque populations. Simons (1963) regards the present multiple species of the genus *Macaca* as recent phenomena, the result of cessation of gene flow between macaque populations of a single species one to three million years ago. The ancestors of present-day *Macaca* probably reached the extremes of their range (e.g. Japan) when continental shelves were exposed during one of the Pleistocene glaciations. Subsequently, rising oceanic levels circumscribed certain macaque populations in island areas (Japan, Philippines, etc.) where, in genetic isolation, they evolved independently of other macaques. Today the phenotypic differences exhibited by the *M. fuscata* subspecies in their biochemical traits, dermatoglyphics and other polygenic systems (Ikeda & Watanabe, 1966; Saheki, 1966), and their unusually high frequencies of certain abnormalities (Morris, 1971), are indicative of a long period of isolation. In fact, some macaque subspecies, such as *M. f. yakui*, may be approaching final speciation marked by reproductive isolation although casual interbreeding with other species might still occur (Hill, 1972; Fooden, 1964).

A further question remains for one who attempts to discuss the possible selective advantages that may be attached to a particular system whether it be a Mendelian biochemical trait or a polygenic (e.g. dermatoglyphic) system. It has been shown that specific dermatoglyphic patterns are related to the elevations of the volar pad and its size and shape at the time of ridge differentiation in the fetus (Midlo & Cummins, 1942). Furthermore, the morphology and size of the volar pads, and thus their dermatoglyphic patterns, appear to be related to locomotor habits. The macaques, a group of quadrupedal monkeys, possess high pattern intensities in the interdigital areas. It should be noted that in the two interdigital areas where both *M. fuscata* subspecies have reached pattern fixation, the whorl has reached 100%. The whorl pattern, of all dermatoglyphic patterns, has the highest intensity value (1.0). This evidence would seem to suggest that if there is selection in macaques for patterns of higher intensity as secondarily related to quadrupedal locomotion, the combination of drift and selection may have operated to fix the whorl pattern. This suggestion is entirely speculative, but one other source of evidence would lend support to the idea of drift and selection operating on particular patterns and areas of the dermatoglyphics. Loesch (1971), using sibship analysis, has suggested that some patterns in interdigital area II and the hypothenar area may be under the control of single genetic loci. It is in these same areas that the *M. fuscata* subspecies have lost pattern variability. Conceivably, loss of alleles at a single locus could occur more rapidly under the combined pressures of drift and selection than loss of a total pattern determined by multiple loci. We are now analysing *M. nemestrina* pedigree dermatoglyphic data, following Loesch's method, in an attempt to establish the heritability indices of the macaque palmar areas, and to test the single-locus hypothesis with reference to the areas in question. Hopefully such a genetic analysis may provide some insight into some of the questions raised here.

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N. Petit-Maire
(with the collaboration of
M. Y. Myassard)

Anterior Alveolar Arch Reduction and Hominid Evolution, with Special Reference to the Position of *Ramapithecus*

Laboratoire de Géologie du
Quaternaire, CNRS,
92190 Meudon-Bellevue, France

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There is no question that anterior teeth reduction and changes in the proportions of the alveolar arch cannot account, by themselves, for the Hominid status of a fossil Primate. One cannot draw conclusions from a single character, even if the chosen quantification is a good test for progressive morphological change. Moreover, one cannot infer systematic position from comparison with mere modern species variation, nor from the limited knowledge of a fossil animal through the characters (even numerous) of a single functional system (the manducator one, in this case).

However, the comparative study of anterior dental arcades in modern and fossil Primates have good phylogenetical value for describing the opposite trends in the *Hominioidea* lines, reflecting different dietary adaptations in Hominids and Pongids.

The relationship, in higher Primates, between the width of the alveolar arch just behind the two P_4 and the corresponding sagittal length (anterior alveolar index) has been studied in former papers. Values for the maxillary arch had not, then, been considered, nor Tertiary Primates included. Publication of complementary data seemed useful. Moreover, due to the courtesy of G. G. Conroy (Yale University), *Ramapithecus wickeri* could be included and its position will be discussed in particular.

Figure 1 shows the evolution of mandibular and maxillar indices throughout time, in the *Hominioidea* (vertically, logarithmic values of time in years; horizontally, indices values).

If we take into account the whole Hominid lineage from *Ramapithecus* to present Man, mandibular index evolution may be represented by a total regression line the inclination of which is -0.156 . Modern Man is well out of the line: thus, we calculated regressions for five groups:

<i>Ramapithecus</i> — <i>Australopithecus</i>	-0.08
<i>Australopithecus</i> — <i>Homo erectus</i>	-0.3
<i>Homo erectus</i> — <i>H. s. neanderthalensis</i>	0
<i>H.s. neanderthalensis</i> — <i>H.s.sapiens fossilis</i>	0
<i>H.s.s. fossilis</i> —Modern Man	0

If we could consider as significant the study of such a reduced sample, we should conclude that no evolution of the character took place since the *Homo* stage was reached. (The mean values and standard deviations for Modern Man are slightly higher than the

Figure 1

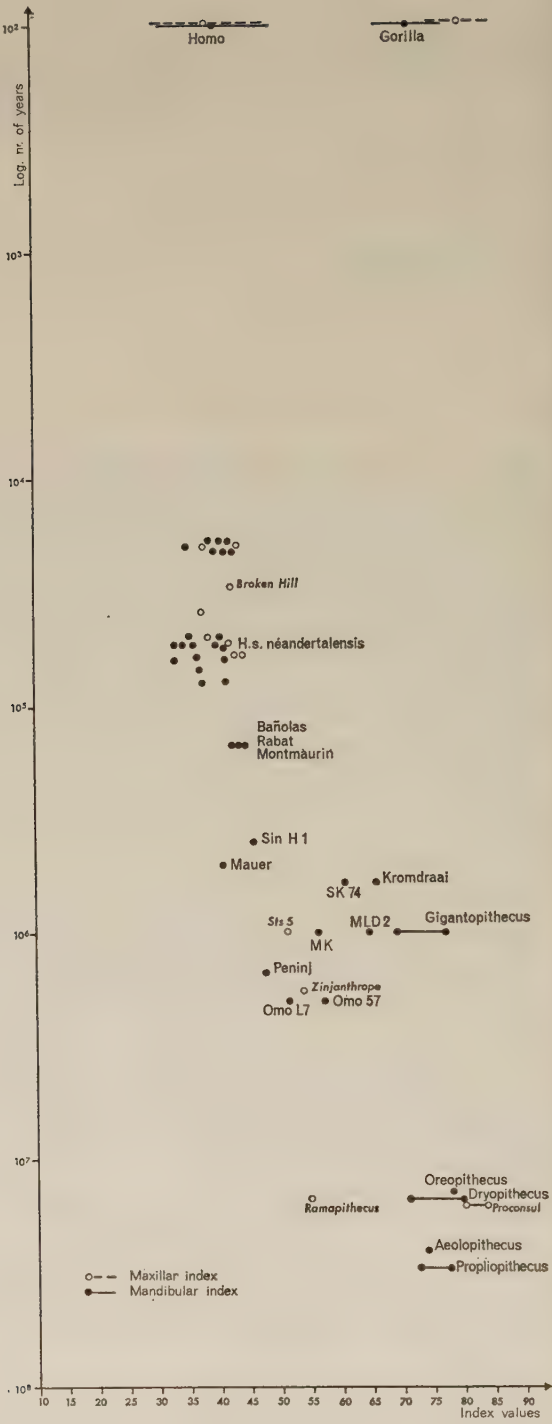


Table 1

Genera	No. of individuals	Mean mand. index	Mean maxill. index	Correlation between md. and mx.
<i>Gorilla</i>	76	79.25 $\sigma = 6.43$	71.57 $\sigma = 7.25$	0.48
<i>Pan</i>	50	68.40 $\sigma = 3.99$	63.52 $\sigma = 6.26$	0.30
Present Man	82	41.3 $\sigma = 4.5$	40.7 $\sigma = 4.7$	0.41

ones obtained for Upper Palaeolithic populations, but no statistical significance can be attached to the fact.)

The correlation ($r = 0.52$) between the mandibular and maxillary indices in *H. sapiens fossilis* is higher than in Modern Man ($r = 0.41$). If the first sample was significant of fossil variation, two interpretations could be given: selective pressure for jaw adjustment must have been stronger in the past ecological context (coarser and tougher diet) than nowadays, accounting for greater harmony between both arches. The progressive destructive process of the human face would appear there. The lowering of correlation could also be due to the change in occlusal pattern.

Both processes may, too, converge to modify correlation. We must await for more valuable fossil series.

The maxillary index is highly correlated with the mandibular one and its evolution is similar, with the same standpoint at the Medium Palaeolithic level. This phenomenon could be due to release of selection pressure after the new main dietary adaptation was gone through.

In the Pongid line, no change in index is to be seen (through our very small fossil sample to our large present sample) from the Dryopithecine stage.

Ramapithecus wickeri (Fort Ternan) falls well out of Miocene and Pliocene Pongid known variation. No error in reconstruction, in our mind, could account for the distance observed. Anyway, even the reconstructed arch published in 1969 by E. Genet Varcin, for *Ramapithecus brevirostris* (shortening of the bi-P₄ width and emphasizing its Pongid characters) gives an index of 65, still far from the Dryopithecine.

Of course, one must wait for further and more complete specimens to conclude upon the taxonomy of *Ramapithecus*, but good probabilities stand for its Hominid status, as far as the manducator system is concerned, as it has already been widely demonstrated by E. Simons *et al.*

The Kanam mandible falls within Australopithecine variation (cf. K. P. Oakley, 1960) for this character, and far enough from Rabat with which P. V. Tobias affianced it in 1962.

Gigantopithecus position confirms its Pongid status (cf. D. Pilbeam, 1970).

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*Laboratoire d'Anatomie Comparée,
Université Catholique de Louvain,
3000 Louvain, Naamsestraat 59,
Belgium*

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Digital pattern type frequencies and frequencies of patterns in the Hypothenar, Thenar/Ist interdigital, IIInd and IIIrd interdigital areas have been used for computing multivariate distances among four human geographical races. Results: Europids and Negrids stand near one another, Mongolids are remote from both and Australids are more remote from the three other races. This pattern of phenetic relationships corresponds to the evolutionary tree of *Homo sapiens* as reconstructed by the author on the basis of palaeoanthropological data.

1. Introduction

Vertical comparison of recent and fossil human osteological material has led the present author (Thoma, 1962–1973) to the phylogenetic conception schematized by Figure 1. The present study attempts to test this phylogenetic conception by analysing recent horizontal dermatoglyphic variation. This way of testing is suggested by the uncommonly rigid and conservative nature of dermatoglyphic variation (Fleischhacker, 1965; Edholm, 1966; Benoist & Dansereau, 1972).

2. Material and Methods

From data of Chamla (1962–63), Ashizawa (1972) and Brehme (1972*a,b*) I computed weighted mean frequencies for the more differentiated male sex (Table 1). Inter-correlations between dermatoglyphic characters are generally weak except main line terminations (Knussmann, 1969). For the latter, however, Ashizawa (1972) does not give frequencies.

In the present study, geographical races are denominated according to the nomenclature of von Eickstedt (1934) and represented by their nuclear groups only, i.e.

Europids: from Europe, Lapps excluded;

Negrids: populations of sub-Saharan Africa; Ful, Ethiopians, Pygmies, Khoisan and the inhabitants of Madagascar excluded;

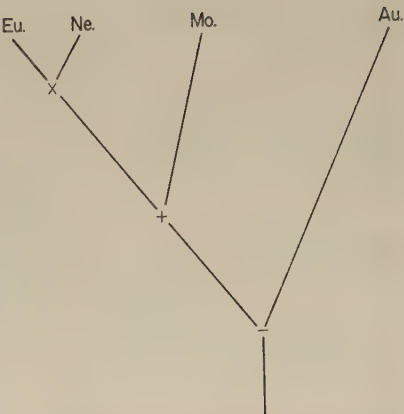
Mongolids: populations of Siberia, Mongolia, Tibet, China, Korea, Japan, Taiwan and Indochina, with exclusion of morphologically non-mongolid peoples;

Australids: the only available complete sample, originating from Arnhem Land (Cummins & Setzler, 1951), is used here with reserves.

As it is shown in Table 1 Mongolid populations display a marked bimodality in the occurrence of patterns in the IVth interdigital area. In consequence, this character must be omitted from further analysis. This latter was performed in two ways.

(1) Percentages have been transformed into angles by means of the C. A. B. Smith formula: $\theta = \sin^{-1} (1 - 2p)$, using the table published by Berry & Berry (1971).

Figure 1. Simplified evolutionary tree of *Homo sapiens* (Thoma, 1962-1973). Recent geographical races: Eu. = Europid, Ne. = Negrid, Mo. = Mongolid, Au. = Australid. Common ancestors: X = Cromagnoid, + = Early Palaeanthropic (cf. Steinheim), - = Pithecanthropoid.



Expression

$$u = \frac{|\theta_1 - \theta_2|}{\sqrt{1/N_1 + 1/N_2}}$$

follows standardized normal distribution. For testing the significance of difference between two percentages, the minimum test value may be obtained when $N_i = n_i$ (= number of individuals) and the maximum when $N_i = 10n_i$ (for digital characters), respectively, when $N_i = 2n_i$ (for palmar characters). The true value of u must lie between these two extremes.

By means of pattern frequencies in the four palmar areas plus digital whorl frequencies I have calculated the mean distance between every two racial samples, according to the formula:

$$MD = 100\sqrt{\frac{\sum_{j=1}^m (\theta_{1j} - \theta_{2j})^2}{m}}$$

where m is the number of characters.

Table 1
Racial frequencies of dermatoglyphic characters (bilateral frequencies for males)

Character		Europids		Negrids		Mongolids		Australids	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Digital	Whorls	244 429	30.0	10 475	29.8	21 549	46.8	90	77.6
Digital	Loops		64.5		63.0		51.2		22.1
Digital	Arches		5.5		7.2		2.0		0.2
Patterns in:									
Hypothenar		9 805	35.9	1 394	25.3	11 630	22.5	90	27.7
Thenar/Ist id. area		10 198	15.6	1 502	17.9	11 769	14.4	90	20.3
IIInd id. area		9 768	5.6	1 666	11.5	11 362	8.5	90	16.3
IIIrd id. area		9 756	48.3	1 691	35.3	11 500	11.4	90	42.3
IVth id. area		9 756	51.0	1 691	76.2	11 683	69.9-84.2* 4.1-14.0†	90	72.4

n = number of individuals examined.
* 13 samples ($n = 4319$).
† 7 samples ($n = 7364$).

(2) By means of presence and absence of patterns in the four palmar areas plus digital whorl, loop and arch frequencies I computed distances under stereographic projection (derived by Edwards, 1971; cf. Constandse-Westermann, 1972). The squared distance between two samples for the j th multiphenotypic character, with S_j degrees of freedom, is

$$E_j^2 = 8 \frac{1 - \sum_{k=1}^{S_j+1} \sqrt{p_{1jk} \cdot p_{2jk}}}{\left(1 + \sum_{k=1}^{S_j+1} \sqrt{\frac{p_{1jk}}{S_j + 1}}\right) \left(1 + \sum_{k=1}^{S_j+1} \sqrt{\frac{p_{2jk}}{S_j + 1}}\right)}$$

and the overall distance coefficient will be

$$E = 100 \sqrt{\sum_{j=1}^m E_j^2 / \sum_{j=1}^m S_j}.$$

From distance matrices I constructed dendrograms by the unweighted average pair group method which seems to reproduce the pattern of relationships most faithfully (Boyce, 1969).

3. Results

Table 2 contains 42 tests of significance between pattern frequencies of the three more representative samples. They will be evaluated on the 1 to 50 significance level. There is only one difference, namely that of whorl frequencies between the Europid and Negrid samples, which is clearly non-significant. Two other differences, namely those of Hypothenar patterns between Negrids and Mongolids and Thenar patterns between Europids and Negrids fall in the doubtful zone. The rest is significant. The best discriminative character is pattern frequency in the IIIrd interdigital area.

Table 2 Tests of significance among pattern frequencies of the Europid, Negrid and Mongolid samples

$u_{[P=0.02]} = 2.326$

Character		Eu.-Ne.	Eu.-Mo.	Ne.-Mo.
Digital Whorls	$\{u \text{ (min.)}\}$	0.401	49.215	29.539
	$\{u \text{ (max.)}\}$ *	1.269	155.630	93.411
Digital Loops	$\{u \text{ (min.)}\}$	3.108	38.184	20.056
	$\{u \text{ (max.)}\}$	9.827	120.748	63.424
Digital Arches	$\{u \text{ (min.)}\}$	6.917	26.870	21.735
	$\{u \text{ (max.)}\}$	21.874	84.970	68.731
Hypothenar	$\{u \text{ (min.)}\}$	8.072	21.588	2.294
	$\{u \text{ (max.)}\}$	11.415	30.530	3.244
Thenar/I	$\{u \text{ (min.)}\}$	2.243	3.579	3.467
	$\{u \text{ (max.)}\}$	3.172	5.062	4.902
II	$\{u \text{ (min.)}\}$	8.071	8.270	3.812
	$\{u \text{ (max.)}\}$	11.414	11.696	5.391
III	$\{u \text{ (min.)}\}$	10.021	61.683	22.428
	$\{u \text{ (max.)}\}$	14.172	87.233	31.719

* $0.75 > P > 0.20$.

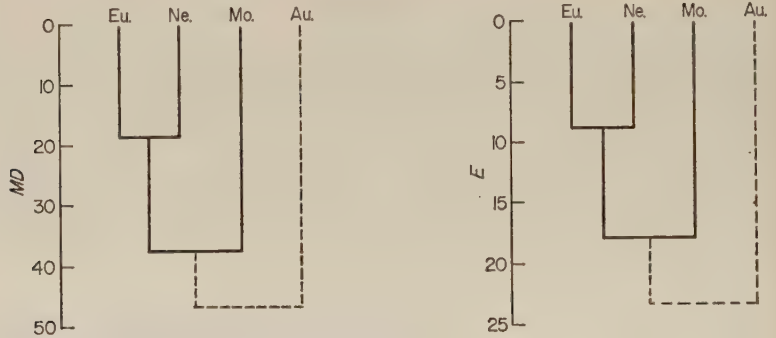
Table 3

Multivariate dermatoglyphic distances (in increasing order) among racial samples

Comparison	<i>MD</i>	<i>E</i>
Negrid-Europid	18.6	8.8
Negrid-Mongolid	31.2	15.3
Europid-Mongolid	43.4	20.5
Australid-Mongolid	45.7	22.0
Australid-Negrid	45.8	23.1
Australid-Europid	48.6	24.1

In Table 3 and Figure 2 both *MD* and *E* indicate the same characteristic similarity pattern: Europids and Negrids stand near one another, Mongolids are remote from both and Australids are more remote from the three other races. This pattern of phenetic relationships corresponds to that of phylogenetic relationships as sketched in Figure 1.

Figure 2. Dendrograms for Table 3.



4. Discussion

Intraspecific phylogeny and taxonomy are never as simple and definite as the scheme adopted here. There are reticulate connections and many transitional and unclassifiable populations. However, by restricting analysis on nuclear groups of such taxa whose fossil history is not totally unknown, I tested only the “skeleton” of our evolution. Results confirm that this skeleton is a real part of the body. Of course, it is not the whole body.

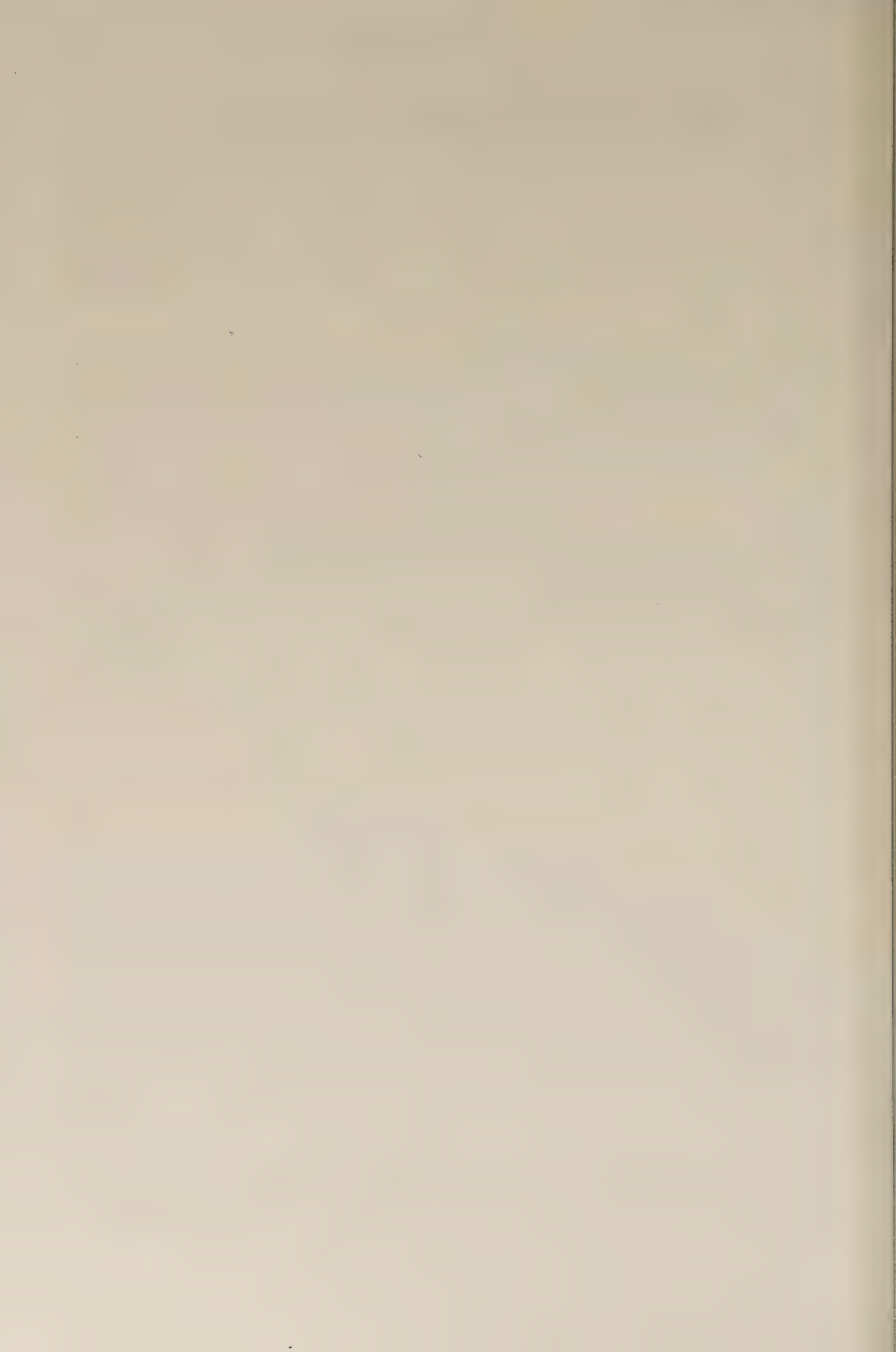
Dermatoglyphic differentiation which follows “inertly” the intraspecific phyletic lines is hardly compatible with systematic selective forces. On the other hand the approximate cube-root shortening of phenetic distances in proportion to time tells in favour of random genetic drift as probable evolutionary mechanism of human dermal ridge system.

5. Conclusion

The correspondence between interracial dermatoglyphic similarity pattern and the evolutionary tree of *Homo sapiens*, as reconstructed by palaeoanthropological methods, increases the probability of the latter.

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D. S. Markarjan
E. P. Isakov
G. I. Kondakov

Intergeneric Hybrids of the Lower (42-Chromosome) Monkey Species of the Sukhumi Monkey Colony

*Institute of Experimental Pathology
and Therapy, U.S.S.R. Academy of
Medical Sciences, Sukhumi, U.S.S.R.*

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A cytogenetic study has been carried out of 2 intergeneric hybrids between *Papio* and *Macaca* genera and 17 hybrids between *Papio* and *Theropithecus* genera, obtained at the Sukhumi monkey colony for the period since 1949 up to 1964. Intermediate or mosaic-intermediate heredity of the phenotypic features of the initial parental species are noted in all the hybrids.

Hybrids between *Macaca* and *Papio* genera resembled baboons according to the body build and colour of eyes, but according to the form of head, face, hair colour, sexual skin and ischial callosities they resembled macaques. More or less domination of the gelade phenotype (head form, location of nostrils, saddle-like nose, hair colour, body build) is seen in the *Papio* × *Theropithecus* hybrids. At the same time, the structure of sexual skin and ischial callosities had an intermediate type between baboons and gelades. Instead of the sexual skin, characteristic of gelades, the appearance of a new feature (hair-free nipple fields up to 6 cm in diameter) has been noted on the chest of the hybrids. The carotype of the hybrids between *Macaca*, *Papio* and *Theropithecus* genera consists of 42 chromosomes, as in the initial species, the homologues of most pairs being significantly similar.

The results of crossings and chromosome study allow one to conclude that African species—hamadryas baboons and gelades—are genetically closer to each other than Asian rhesus macaques and African hamadryas baboons, having been isolated from one another geographically for a long period of time. In this connection, intergeneric hybrids between *Papio* and *Theropithecus* genera are obtained more easily and the hybrid retains fertility unlike the non-fertile hybrid between macaques and baboons, which is obtained with difficulty.

1. Introduction

Publications describing cases of intergeneric hybridization of the lower monkeys are not numerous. Zuckermann (1933) gives the following list of intergeneric hybrids of the lower monkeys:

- (1) *Macaca irus* ♂ × *Mandrillus sphinx* ♀ (1878).
- (2) *Macaca irus* ♂ × *Mandrillus leucophaeus* ♀ (1904).
- (3) *Macaca nemestrina* ♂ × *Papio porcarius* ♀ (1862).

Nesturch (1934) reports about a successful cross-breeding between mandrill male and mangabey female at Cologne Zoo. In Leningrad there was another intergeneric hybrid between baboon and rhesus monkey (Voronin, 1950). Analysis of these data shows the fact that all the intergeneric hybrids described were obtained from the 42-chromosome monkey species. Not a single case of a reliable description of intergeneric hybrids between species with different chromosome number has been given. It is well known that in the course of evolution the differentiation of species into new ones is sure to be accompanied by changes in the gene pool and often in the caryotype, that finally lead to the genetic isolation of species and the failure of getting offspring from them. That is why the results of intergeneric cross-breedings may be of great value in the analysis of the divergent degree of species. Structural chromosome rearrangements, occurring in

the course of species evolution, cause either the failure in crossing of individuals in population or lead to the decrease of fertility and the hybrid zygote viability due to the gene balance disturbances (Dubinin, 1970).

Structural chromosome rearrangements are given a particular place in the evolution of karyotypes and genotypes in Primates (Chu & Bender, 1961; Chiarelli, 1966, 1967). According to the literature (Chiarelli, 1967) all the species of *Macaca*, *Papio* and *Theropithecus* genera have the same chromosome number ($2n = 42$), total chromosomal length, similar types of chromosome pairing (metacentric and submetacentric), and similar marked (satellite) chromosomes. All the genera are interbred and this fact testifies to their relative genetic affinity (Chiarelli, 1967; Egozcue & Egozcue, 1967). At the same time, the high frequency of unsuccessful outcome of pregnancies in cases of intergeneric hybrids points to the presence of certain differences in their genotype (Chiarelli, 1961). Idiogram comparison of *M. mulatta*, *P. hamadryas* and *Theropithecus gelada* species has revealed certain differences in size and position of centromeres of some chromosome pairs (Chiarelli, 1962).

These data, however, are to be considered as preliminary, since they have been obtained without taking the chromosomal heteromorphism in the metaphase plates with a different degree of spiralization into consideration (Gindilis, 1966). These technical obstacles are also aggravated by the difficulty of selection and comparison of the homologues in the 2-6 and 7-13 chromosome groups, due to the great similarity of neighbouring pairs.

Everything stated above suggests, that the real difference in karyotypes between macaques, baboons and gelades can be more or less distinguished from that noted earlier. More exact evaluation of similarity and difference between chromosomes of these species can be obtained by the study of chromosome behaviour at meiosis in intergeneric hybrids. However, such a possibility has been rather problematic so far, due to

Table 1 Intergeneric hybrids of the Sukhumi monkey colony

Parents	Name	Sex	Date of birth	Fertility
(1) ♂ (<i>M. mulatta</i> × <i>M. lapunder</i>) ♀ <i>Papio hamadryas</i>	Prima	♀	10.3.1949	Sterile
	Marquise	♀	2.12.1949	Sterile
(2) ♂ <i>P. hamadryas</i> × ♀ <i>T. gelada</i>	Piogela	♀	10.12.1950	2 still-borns
(3) ♂ <i>T. gelada</i> × ♀ <i>P. hamadryas</i> (10 different females)	Eicera	♀	28.1.1960	6 pregnancies, 1 alive
	Kkan	♂	21.9.1960	fertile
	Elemira	♀	25.11.1961	4 pregnancies, 1 alive
	Garbina	♀	7.5.1962	4 pregnancies, no alives
	Apsheron	♂	7.2.1962	Not crossed
	Balhash	♂	6.3.1962	Not crossed
	Vesuvius	♂	4.10.1962	Not crossed
	Ginseng	♂	22.7.1963	Not crossed
	Bich	♂	3.8.1963	Not crossed
	Eileron	♂	5.8.1963	Not crossed
	Balada	♀	27.8.1963	Not crossed
	Guravka	♀	19.10.1964	No data
	Trostinka	♀	28.12.1964	2 pregnancies, no alives
(4) ♂ <i>T. gelada</i> × ♀ <i>P. anubis</i>	Spartakiada	♀	15.8.1961	Not crossed
	Kortes	♂	19.6.1963	Fertile
	Sputnik*	♂	21.9.1959	Fertile

* Offspring as a result of crossings with hybrid (*Papio* × *Theropithecus*) females is not viable. Offspring as a result of crossings with *Papio hamadryas* females is viable.

the rarity and the value of such hybrids. Apparently, reliable data concerning the degree of morphological similarity and difference between homologous chromosome pairs could be obtained as a result of their comparison in one hybrid somatic cell, where chromosome morphology variability is expressed to a lesser extent, as compared with the cells with a different degree of chromosome spiralization (Gindilis, 1966) (Table 1).

2. Materials and Methods

Investigation has been carried out on 17 double and 2 triple intergeneric hybrids between *Macaca*, *Papio*, and *Theropithecus* genera. Table 1 presents the characteristics of the hybrids employed. We have used genealogical, clinical, and morphological data of the hybrids and their offspring. For evaluating the character of the phenotypic signs of inheritance such indices as the head form, location and form of nostrils, appearance of the hair coat, the colour of eyes, shape of the tail, the structure of the sexual skin, and ischial callosities were used. Chromosome comparison has been carried out only in the somatic cells for the reason that one triple intergeneric/(*Macaca rhesus* $\times$ *Macaca nemestrina*) $\times$ *Papio hamadryas*/hybrid (Marquise) was a sterile female and another double intergeneric *Theropithecus gelada* $\times$ *Papio hamadryas* hybrid (Ginseng), was a reserve valuable male, from the breeding standpoint. Chromosomes were obtained from bone marrow and leucocyte culture cells by the earlier described methods (Markarjan & Machavariany, 1969). Chromosomes have been arranged according to the system described earlier (Chiarelli, 1966) with a slight modification, which consisted of the disposition of satellite (marked) chromosome to the large metacentric group, because in the plates with amphiplasty of satellites these chromosomes had a shape approximating metacentrics. Chromosome pairing has been carried out according to the principle of maximal similarity, taking into account the exceptional importance of this procedure for further analysis of chromosome similarity. Chromosome measurement has been carried out with the help of the binocular MBS-I lens with the smallest point of its ruler of 0.1 mm. Since it has never been possible to note the absolute homologous identity according to parametric criteria (Gindilis, 1966), we have conditionally assumed that the homologues differed from each other, when they differed in relative length not less than by 0.6% or in the centromeric index not less than by 3.0%.

3. Results and Discussion

Obtaining of hybrids

Intergeneric hybridization of monkeys at the Sukhumi monkey colony was begun in 1948, and in the course of the period up to 1964, 22 intergeneric hybrids (Table 1) from the 42-chromosome species have been obtained (Isakov, 1965; Markarjan *et al.*, 1972). All the attempts to obtain hybrids between species with different chromosome number (for instance *Macaca* $\times$ *Cercopithecus* and others) were unsuccessful. Intergeneric hybridization at the Sukhumi colony was preceded by a great experience in the field of interspecific hybridization. During the period from 1932 up to 1949, 47 interspecific hybrids from different species of *Macaca* and *Papio* genera (Lakin, 1949) had been obtained. Though an intergeneric hybridization in Sukhumi had a purposeful character, it was still scanty. That is why we had no opportunity to study all the possible crossing

variants. Intergeneric, as well as interspecific crossings, pursued the following objects: (1) The study of crossing possibility between different monkey species and genera. (2) The increase of stability and viability of monkeys under the climatic conditions of the Sukhumi colony. The first interspecific hybrids in fact already possessed all the features of hybrid heterosis: more massive body proportions, great endurance, high resistance against pneumonia and enterocolitis, which are the most frequent causes of deaths among monkeys at the colony. (3) Preservation of gelades, which did not breed at the colony.

The intergeneric copulations went on easily, without any artificial methods, by means of the usual placing of male and female in one cage. Cases of sexual antipathy or frigidity, according to the generic sign, were not noted.

Repeated attempts to obtain hybrids between non-hybrid macaques and baboons utterly failed. Nevertheless, on 10 March 1949, the first intergeneric female-hybrid (Prima) was born in Sukhumi as a result of mating of *Macaca mulatta* $\times$ *Macaca nemestrina* interspecific hybrid male and *Papio hamadryas* female. On 2 December 1949, the second female (Marquise) was born from the same parents. She is in good health now at the age of 24 years. Both hybrids are sterile females, with irregular menstrual cycle, reluctantly covered both by macaque and baboon males. The employment of the interspecific hybrid male might have possibly served the successful intergeneric hybridization between *Macaca* and *Papio* genera. Data are available (Chiarelli, 1962) regarding the fact, that, among macaques, *Macaca nemestrina* (native land is Indochina) have the greatest caryotype likeness to that of hamadryas baboon, which possibly made the intergeneric hybridization between macaques and baboons easier.

The first hybrid crossings between *Papio* and *Theropithecus* genera began in 1950. A hybrid female from hamadryas baboon male and gelade female was born that year (Table 1). In 1959 females of *P. hamadryas* and *P. anubis* were placed with one gelada male (Celebes). In the course of these matings 26 pregnancies, 7 (27%) of which have ended in abortions and still-borns, have occurred, this being somewhat above the level of abortions and still-borns (up to 20%) among monkeys during interspecific crossings (Asanov, 1969); 19 have ended in deliveries of healthy offsprings. The majority of these offsprings have been alive up to the present time. Part of them are kept at the Sukhumi colony, and some in the different zoos of the Soviet Union.

Characteristics of the hybrids

Tables 2 and 3 present a comparative illustration of the characteristics of the phenotypical features of intergeneric hybrids. Analysis of these data indicates the complicated character of heredity. It should be noted that intergeneric F^1 *Papio* $\times$ *Theropithecus* hybrids are characterized by the intermediate heredity of the most phenotypic features, gelade's phenotype domination, however, being well expressed. As for the intergeneric F^1 *Macaca* $\times$ *Papio* hybrids, they can be characterized by the mosaic-intermediate heredity, as a result of which the hybrids resembled macaques according to the head form, structure of sexual organs, ischial callosities, and hair colour; but according to the body build, its measurements, form of the tail and colour of eyes, they resembled hamadryas baboons. As it was noted above, those females were highly viable, but sterile. At the same time, all the intergeneric *Papio* $\times$ *Theropithecus* hybrid females were fertile (Table 1), though they revealed a high frequency of pregnancy and delivery pathology, when mating with the same hybrid male (Sputnik) (paternal line). Of 17

Plate 1. ♀ Hybrid/♂ (*M. mulatta*
× *M. nemestrina*) × ♀ *Papio*
hamadryas/(Marquise).



Plate 2. Female hybrids (♂ *Theropithecus gelada* × ♀ *Papio hamadryas*).



Plate 3. Male hybrid (♂ *Theropithecus gelada* × ♀ *Papio hamadryas*).



Plate 4. Caryotype of the ♀ hybrid/♂ (*Macaca mulatta* × *Macaca nemestrina*) × ♀ *Papio hamadryas*.

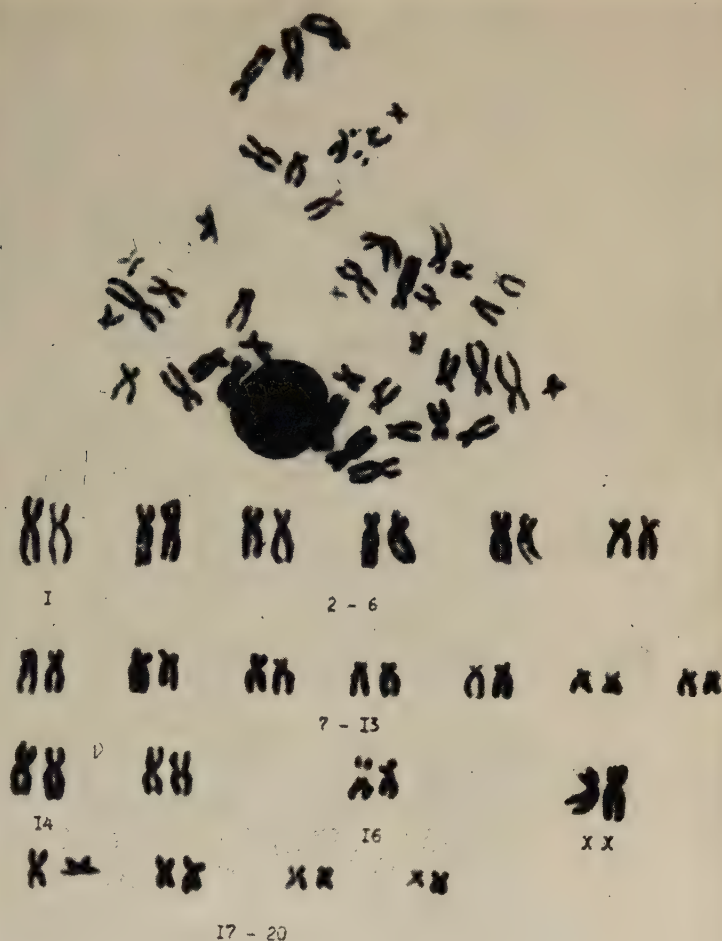


Plate 5. Caryotype of the hybrid (*Theropithecus gelada* $\times$ *Papio hamadryas*), male.

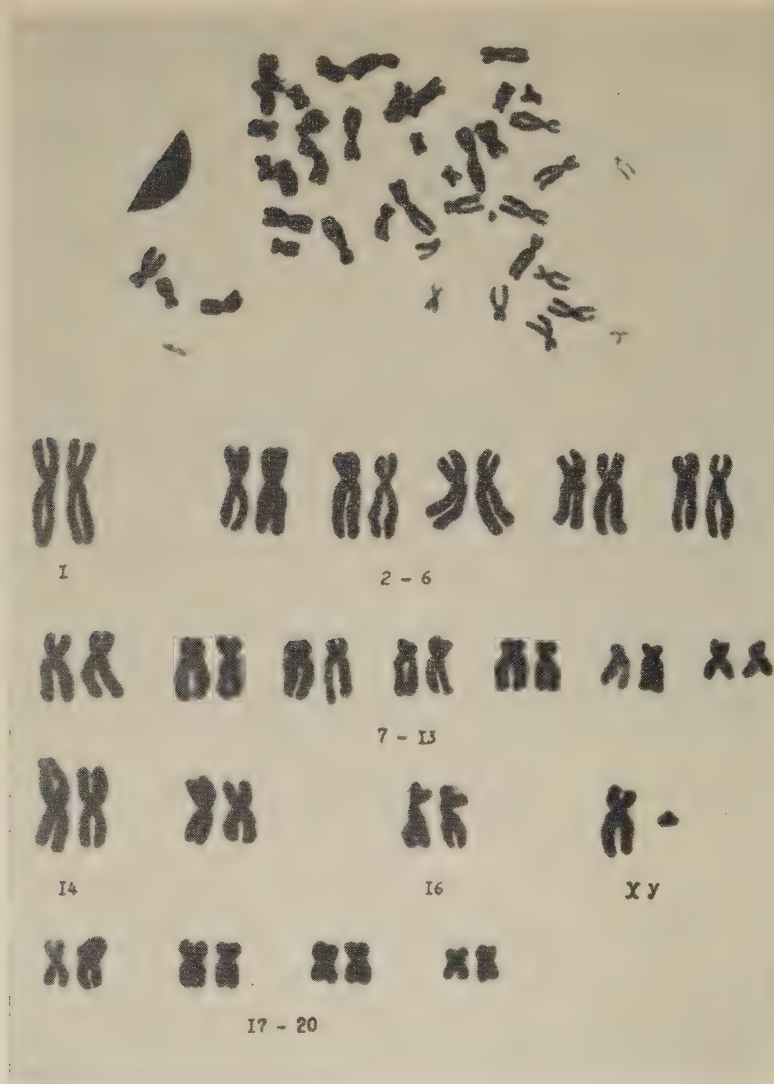


Table 2

Comparison of the phenotypic features of *Papio* and *Theropithecus* and their hybrids

<i>Papio hamadryas</i>	<i>Theropithecus gelada</i>	F ¹ hybrids
(1) Oblong face, dog-like head. Hair free face. Nostrils located at the end of muzzle. Longitudinal bony wall on both sides of face.	(1) Head roundish. Face shortened, hair free. Nostrils located on the muzzle's sides, higher than in baboons, the brims of the nostrils are bulging out. There are rounded eminences instead of the bony walls.	(1) Head roundish, face shortened, nostrils are located high as in gelades. One can distinguish several types with different degree of domination of the gelada features.
(2) Hair covers the whole of the body except buttocks, palms, and soles. Colour dark-grey. Male has a fluffy grey mane.	(2) There are hair-free parts on the neck and chest unlike in baboons. Hair dark-brown. Male has a fluffy mane.	(2) Hair dark-brown, colour and structure more like gelada's hair. Male has a fluffy mane. There are no bare parts on the neck and chest, unlike gelades.
(3) Skin fair.	(3) Skin fair, hair-free parts on the chest dark-pink in colour.	(3) Skin fair. There is no pigmented area on the chest.
(4) Sexual skin of females highly developed, swells heavily during the sexual cycles.	(4) Sexual skin divided into several parts—genito-anal, suprapubic, cervico-pectoral, and looks like a chain of small sexual elevations, reminding sand-glass.	(4) No sexual skin on the chest. There are hair-free nipple areas up to 6 cm in diameter (baboons and gelades do not have them). The structure of the genito-anal area is intermediate between baboons and gelades.
(5) Ischial callosities highly developed, red-pink in colour. It swells heavily during the sexual cycles in females.	(5) Ischial callosities considerably smaller in size, than in baboons. They are separate roundish parts of the keratosis skin of dark-grey colour.	(5) The form and the structure of the ischial callosities is somewhat intermediate between baboons and gelades. They are roundish areas of the keratosis skin connected with each other (they are not connected in gelades).
(6) Fertility is high.	(6) Fertility low at the Sukhumi monkey colony.	(6) Fertility low.
(7) Range area—Africa (Ethiopia, the Sudan, Arabia).	(7) Range area—Africa (Ethiopia).	

pregnancies of 7 hybrid females, as a result of these crossings, only 2 hybrids of the second generation have proved viable without apparent signs of heterosis. Along with this, crossings between the same hybrid male Sputnik and 2 non-hybrid hamadryas baboon females have resulted in 5 pregnancies which ended in the birth of healthy and viable offsprings.

Analysis of these data show that the hybrids between baboons and gelades were obtained more easily and retained fertility, thereby deviating from the non-fertile hybrids between *Macaca* and *Papio* genera, obtained with great difficulties. This allows us to assume the existence of a great genetic affinity between baboons and gelades (native land—Africa, Ethiopia), rather than between macaques (native land—Asia) and baboons (native land—Africa).

Caryotype of the hybrids

The modal number of chromosomes in two investigated intergeneric ♂ (*Macaca mulatta* × *Macaca nemestrina*) × *Papio hamadryas* ♀ and ♂ *Theropithecus gelada* × *Papio hamadryas*

Table 3

Comparison of the phenotypic features of *Macaca* and *Papio* and of their hybrids

<i>Macaca mulatta</i>	<i>Papio hamadryas</i>	<i>F</i> ¹ Hybrid ♂ (<i>M. mulatta</i> × <i>M. nemestrina</i>) × ♀ <i>Papio hamadryas</i>
(1) Head moderately oblong, roundish, nose short. Nostrils located high and looking like chinks.	(1) Head oblong and looking like a dog's head. Nostrils at the end of muzzle, oval in shape.	(1) Head oblong as in baboons, but the nose is short and rounded as in macaques. Nostrils located high, oval in shape.
(2) Eyes yellow.	(2) Eyes hazel.	(2) Eyes light-hazel.
(3) Hair grey at the roots, and yellow at the ends. Hair on the stomach light-grey.	(3) Hair grey or dark-grey.	(3) Hair dark-grey at the roots and yellow at the ends, as in rhesus macaques.
(4) Tail short (up to 25 cm).	(4) Tail long (up to 50 cm) with the brush at the end.	(4) Tail similar to that in baboon, but is shortened up to 35 cm, with the brush at the end.
(5) Sexual skin weakly developed and swells moderately. Genito-anal area red. During the sexual cycles the redness takes the whole of the pelvic area.	(5) Sexual skin of the females is highly developed and swells heavily during the sexual cycles. It is light-red in colour.	(5) Sexual skin weakly developed (as in macaques). There is a small patch of redness in the genito-anal area.
(6) Ischial callosities moderately developed in the shape of two roundish keratosis plates of grey colour.	(6) Ischial callosities highly developed, red-pink in colour. They swell heavily in females during the sexual cycles.	(6) Ischial callosities weakly developed as in macaques. They are like two roundish plates of the keratosis skin of grey colour.
(7) Fertility high. Cycles are regular.	(7) Fertility high. Cycles are regular.	(7) Sterile. Cycles are not regular, lengthened up to 2-3 months, oligomenorea.
(8) Range area—Asia (India, Indo-China).	(8) Range area—Africa (Ethiopia, the Sudan, Arabia).	(8) According to size and body build the hybrid looks like a baboon, and according to the head form, hair colour, sexual skin and ischial callosity structure it looks like a macaque.

/♀/ hybrids was 42, as in the initial species. The level of chromosome aberrations (Table 4) remained within the usual spontaneous values (Markarjan *et al.*, 1971). During the caryotype mapping, however, the number of the non-homologous chromosome pairs in the cells of the hybrids came to be higher compared to that of non-hybrid animals (Table 5). The greatest difficulty has arisen when mapping the chromosomes of the triple hybrid (Marquise). This hybrid systematically showed the non-homology of two submetacentric chromosome pairs in group 2-6, and one pair in group 7-13, and the metacentric pair No. 15. This difference applied both to size and location of the centromere. It is known (Gindilis, 1966), that even the non-hybrid individuals may have morphological differences between homologues. The high frequency of non-homology of the first chromosome pair in rhesus macaques is indicated in Table 5. However, the average number of non-homologous pairs in cells and the average difference of homologues according to the centromeric index in the hybrids investigated here have proved higher than in non-hybrid monkeys. This should, apparently, be explained not only by the usual heteromorphism of the homologues, but also by the real difference between the homologues of some chromosome pairs in species belonging to *Macaca*, *Papio*, and

Table 4 Chromosome characteristics of macaques, baboons, and intergeneric *Macaca* × *Papio* and *Papio* × *Theropithecus* hybrids

Species	No. of indiv. studied	No. of metaphase studied	Chromo- aberrations observed	Chromosome number per cell										Sex chromosomes	Fertility
				21	30	35	40	41	42	43	50	84	>85		
<i>Macaca mulatta</i>	16	1127	1.5 ± 0.3	1	2	3	45	63	1004	1	0	2	8	XX XY	Normal
<i>Papio hamadryas</i>	17	1798	1.5 ± 0.3	1	2	8	55	86	1640	1	0	4	1	XX XY	Normal
<i>Macaca</i> × <i>Papio</i> hybrid	1	83	2.4 ± 1.7	0	2	0	11	2	65	2	0	1	0	XX?	Sterile
<i>Papio</i> × <i>Theropithecus</i> hybrid	1	100	3.0 ± 1.7	0	0	0	4	7	89	0	0	0	0	XX XY	Low

Table 5 Caryotypic analysis of Rhesus Macaques and the hybrids between *Macaca* × *Papio* and *Theropithecus* × *Papio* genera

Monkey species	Number	Metaphase number	Number of metaphases with odd numbers of chromosomes	Average number		Average difference of homologues according to the relative length (%)		Average difference of homologues according to the centromeric index (%)	
				of nonhomologous pairs per cell	per cell	1-2	1-6	1-2	1-6
<i>Macaca mulatta</i>	4	13	9	1.2 ± 0.4	0.85	0.95	0.75	3.8	5.7
<i>Macaca</i> × <i>Papio</i> hybrid	1	14	12	2.9 ± 0.7					
<i>Theropithecus</i> × <i>Papio</i> hybrid	1	14	10	2.0 ± 0.6					

Theropithecus genera. The highest frequency of non-homologous pairs per cell (2.9%) has been found in the *Macaca* $\times$ *Papio* hybrid, which was noted to be completely sterile (Table 5, Plate 4). An intermediate position according to the frequency of non-homologous pairs belongs to the hybrids between baboons and gelades, which are fertile, but yield to the initial species in this respect. The latter systematically display the presence of non-homologous submetacentric chromosomes in group 2-6 and in the metacentric chromosome pair No. 14 (Plate 5). As a result of statistical analysis the reliability of the revealed differences in homologous chromosomes is not high. Thus, the revealed morphological differences in some chromosome pairs in the hybrids should be regarded as weakly pronounced. We hope that future investigations of meiosis will reveal more differences in the chromosome homologues.

4. Conclusion

- (1) Investigated intergeneric hybrids show, as a rule, intermediate and more rarely mosaic heredity of the phenotypic features of the initial parental species.
- (2) Hybrids between *Macaca* $\times$ *Papio* genera resemble baboons according to the body build and colour of eyes, but according to the head and face forms, hair colour, structure of the sexual skin and ischial callosities they resemble macaques.
- (3) Gelade phenotype more or less dominates in the hybrids between *Papio* $\times$ *Theropithecus* genera (head form, location of nostrils, hair colour, body build). At the same time, the structure of the sexual skin and ischial callosities was intermediate between baboons and gelades. Instead of the sexual skin, typical for gelades, the appearance of a new feature (hair-free nipple fields up to 6 cm in diameter) has been noted on the chest of the hybrids.
- (4) The karyotype of the hybrids between *Macaca*, *Papio*, and *Theropithecus* genera consists of 42 chromosomes as well as in the initial species, the homologues of the most pairs being significantly similar.
- (5) African species of hamadryas baboons and gelades are genetically closer to each other, than Asian rhesus macaques and African hamadryas baboons, having been isolated one from the other geographically for a long period of time. In this connection, intergeneric hybrids between *Papio* and *Theropithecus* genera are obtained more easily and the hybrids retain fertility, thereby differing from sterile hybrids between macaques and baboons which are obtained with difficulty.

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Sub-Department of Anthropology,
British Museum (Natural History),
London, England

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Cranial and femoral fragments of five hominids were recovered in 1932 from exposures of Middle Pleistocene lake-beds at Kanjera on the S. shore of the Kavirondo Gulf, Kenya. L. S. B. Leakey considered that the hominids were contemporaneous with the fauna of the lake-beds, and this view seemed to be supported by results of applying the fluorine method of relative dating. Comparison of the hominids and fauna by means of radiometric assay indicates that the hominids are considerably younger.

In March and April 1932, L. S. B. Leakey and members of his expedition discovered a number of human cranial and femoral fragments in exposures of Middle Pleistocene lake-beds at Kanjera on the S. shore of the Kavirondo Gulf, N.E. part of Victoria Nyanza, Kenya. Five hominids were represented, Kanjera 1-5. Some of the cranial fragments were reported as found *in situ*, but others were found on the surface of the lake-beds exposed in erosion gullies. The fauna in the lake-beds (representing the Kanjeran stage) include *Elephas recki*. Radiometric assays of the human bones and Kanjeran fauna gave the following results:

Kanjera 3, orbital fragment, <i>in situ</i>	eU308 = 15 parts/million
rt parietal fragment, <i>in situ</i>	21
cranial fragments from surface	16, 27, 27, 30, 42
femoral fragment from surface	8, 14
Kanjera 4, frontal fragments from surface	11, 21, 35
Kanjeran faunal fragments	26, 131, 146, 159, 216

Chemical analyses gave the following results:

Kanjera 3, parietal fragment	$F = 1.3\%$	$100F/P205 = 6.0$	$N = \text{nil}$
Kanjera 4, frontal fragment	$F = 2.0\%$	$100F/P205 = 13.5$	$N = 0.01\%$
Antelope horn-core, Kanjeran	$F = 0.5\%$	$100F/P205 = 6.0$	
Antelope metapodial, Kanjeran	$F = 3.4\%$	$100F/P205 = 10.0$	$N = \text{nil}$
Chelonian bone, Kanjeran	$F = 2.4\%$	$100F/P205 = 9.0$	$N = \text{nil}$

Comparison of the fluorine content of the human bones from Kanjera with that of the Kanjeran fauna supported the provisional conclusion that they were contemporaneous. However, it is now known that in volcanic areas (particularly under tropical conditions) fluorine analysis does not provide a reliable method of relative dating. Comparison of radiometric assays is much more indicative. Although there is a slight overlap between the ranges of eU308 in randomly selected examples of Kanjeran fauna and the hominid bones from this site, the disparity between the *averages* of the two groups is so great (hominids 22 parts/million, fauna 136 parts/million) that it is difficult to believe any longer in their contemporaneity. Kanjera 3 was recorded as "partly *in situ*", Kanjera 1 was described as a "surface find", Kanjera 2 as "near surface", Kanjera 4 as "surface".

When deposits such as the Kanjera beds become waterlogged during the wet season, bones lying on the surface readily become incorporated, so that when subsequently discovered they can easily have the appearance of occurring *in situ*.

Thus on the basis of reviewing all the radiometric assays that have been carried out it is now inferred that the Kanjera hominids, although fossilized (Upper Pleistocene?), are considerably younger than the Kanjeran faunal stage (= Middle Pleistocene) to which they have been referred in all previous publications. This conclusion is supported by the presence of measurable traces of collagenous residue in Kanjera 4 (as indicated by 0.01 % N in washed sample), whereas in neither of the two samples of Kanjeran fauna was any detected.

The specimens from Kanjera on which these results were obtained are preserved in the Department of Palaeontology, British Museum (Natural History), with the exception of the fragment of the skull Kanjera 4 which was given to the author by Dr L. S. B. Leakey in 1947 for the purpose of experimental analysis.

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E. Genet-Varcin

Université Paris VI.
Laboratoire de Paléontologie des
Vertébrés et de Paléontologie
Humaine, 4 Place Jussieu,
75230 Paris, France

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accepted 20 November 1973

Platyrrhine Contribution to the Phylogeny of the Primates

The morphology of the skeleton of both extant and fossil Platyrrhini often suggests an image of the ancestry of higher Primates, Man included. Here we give a survey of the characters of common origin to both groups. Reciprocally, a number of such original characters are seen to be maintained in modern Man, thereby placing him along a direct and singular evolutionary lineage.

In 1969, Lavocat forwarded the view that rodents from South America may have had an African origin. The same year, Hoffstetter brought to light the presence, in a deposit in Bolivia, of a primitive platyrrhine Primate, *Branisella*, dating back to the lower Oligocene. He soon added fresh support to Lavocat's thesis, by stating that Primates from South America might have had a biological history identical to the Caviomorphae, presumably of African origin (1969, 1970, 1971, 1972).

As a matter of fact, zoologists have always related South American monkeys to those of the Old World. They even group them in the same suborder, namely, Simii (Van der Hoeven, 1833); Anthropoidea (Mivart, 1864; then Simpson, 1945); Simiae (Haeckel, 1866); Pithecoidea (Pocock, 1918; then Hill, 1957). However, Arambourg (1948) severs the monkeys (Simii) from Hominines (Hominini) though leaving Ceboidea, Cercopithecoidea and Pongoidea within the same suborder [see Hill (1953) for the literature]. All these workers thus arrive at the view that, in general, the platyrrhines are nearer than prosimians to the higher Primates.

Notwithstanding such a connection, the above authors believe that the platyrrhines arose from a stem localized in North America from where the earliest forms would have reached the South American continent, whereas the ancestors of the catarrhines were presumably Euroasiatic. However, Elliot-Smith (1903) had noticed the similarities existing in the brain between platyrrhines and lorisiformes, and Regan (1930) showed the analogy between platyrrhines and lorisiformes on the evidence of their dental enamel structure. This being the case, the two groups might have stemmed from a common Euroasiatic ancestor.

For a long time we have also been struck by the existence, in the platyrrhines, of features which in the catarrhine ancestors appear not to have ever been replaced, thereby implying a common origin of the two groups. And, though it might be paradoxical, it is in the genus *Homo* that the concurrence of these plesiomorphic traits are most numerous. Indeed, this paradox may be explained by the fact that *Homo* has retained a variety of primitive characters while undergoing specialization in other particular traits.

We wish therefore to draw attention to those features which, being shared by platyrrhines and catarrhines, witness their derivation from the same stem, as a result of having lived together a long time in the Old World. Another radiation is thus implied, possibly starting from Africa.

Let us sponsor the hypothesis that platyrrhines and catarrhines had a common Euroasiatic ancestor in the form of a very primitive form which could also fit the loriformes, as shown by the structure of the otic region, which differs in all of them from that observed in the lemuriformes (Szalay, 1972).

If *Alsaticopithecus* and *Amphipithecus* do exhibit the tendency to eliminate the anterior premolars, the postulated primitive Primate must have presented a more generalized condition of these two teeth.

From a palaeogeographic point of view, this hypothesis implies that the common ancestor reached Africa at a very early time; either in the upper Cretaceous when the great adaptive prosimian radiation must have been under way, or in the Paleocene or the early Eocene: in any event, much earlier than the Oligocene, since at that time in Bolivia the settling of *Branisella* was taking place, while the spread and above all the blossoming of platyrrhines occurred in the Miocene, when their differentiation was perhaps more important than it is at present (Hershkovitz, 1970).

At any rate, loriform differentiation, too, had been ascertained in Africa in the Miocene, at which time the Galagides were already specified (the lorid presence in Asia might be explained by the bipartition of their stock prior to their emigration into Africa, or by a mio-pliocenic migration associated with that of other Primates).

Supposing this passage of Primates (and rodents) from Africa to South America occurred, it would have taken place much earlier than the lower Oligocene, as claimed by Hoffstetter, due probably to a slight drift of the two continents and the existence of equatorial currents from east to west, facilitating passive transport. The same pattern of passive transport must explain the colonization of Africa through the Tethys, which attained its greatest extension some 65 million years ago, namely in the Paleocene (Phillips & Forsyth, 1972).

From the anatomical viewpoint, the platyrrhines, even extant ones, have retained a wide variety of generalized structures reflecting an ancestral condition. Actually, they display an evolutionary parallelism to the catarrhines, which may be accounted for by a common origin.

Their very small body size and the subequality of their limbs are to be considered ancestral traits. Except in *Ateles*, the forelimbs are shorter than the hindlimbs. The intermembral index $\text{length(humerus + radius)} \times 100 / \text{length(femur + tibia)}$ varies, on an average, from 75 to 81, while in *Homo* it varies from 66 to 73. The lower value of this index in *Homo* may be explained by the elongation of its lower limbs, a unique feature among Primates. As regards *Ateles*, despite the fact that it attains a value of 104 for this index, it is however able to walk with an erect posture, with an amazing bipedal gait, mimicking, for instance, the gibbon. It may also be recalled that a human baby crawling on all fours places its hands flat on the ground the way monkeys do, first among these the platyrrhines, in which the hand has not undergone adaptive changes.

The thumb, unless it has disappeared as in *Ateles* and *Brachyteles*, is comparable in length with the human thumb, in that it reaches the proximal interphalangeal articulation, whereas in the other Simii it was generally shortened. The other fingers have the primitive formula $\text{III} > \text{IV} > \text{II} > \text{V}$, which is the human formula also. The limb bones are straight and the astragalus proportions are close to those in Man. Lastly, in *Ateles* and *Alouatta* the trunk enlarges to a considerable extent.

In turn, the platyrrhine skull displays a number of poorly specialized traits, reconcilable with a very early evolutionary phase which, of course is close to foetal morphology.

We shall call attention first of all to its rounded shape, the lack of bony superstructures in the braincase and the marked facial reduction. These characters, compatible with those of a human ancestor, account for Ameghino's reaction when discovering them in the fossil platyrrhine from the Miocene which he named *Homunculus*.

We shall reexamine in greater detail those platyrrhine structures that may be considered plesiomorphic. Their faces are short with respect to the skull, averaging only $\frac{1}{4}$ the length of the bony head. Simons (1971) observed that *Apidium phiomense* (Fayoum Oligocene) also has a short face recalling that of marmosets. The frontal region of platyrrhines is convex, and its vertex is always higher than the orbital roof even in *Homunculus*; in *Saimiri* theinion lies near the Frankfurt plane, this character being encountered only among some hominids (*Oreopithecus*, *Australopithecus*, *Homo sapiens sapiens*); the *foramen magnum* lies forward under the skull; the supraorbital sagittal and occipital ridges are missing. At the level of the otic region the absence of a bony tympanic duct characterizes the platyrrhines. Now, a similar otic pattern in *Aegyptopithecus* (Fayoum Oligocene) was brought to light by Simons (1967). Hence, all the higher Primates would have undergone a structural phase identical to that observed among lorisiformes, in which the tympanic ring sets the opening of the middle ear. Taking into account the body size, the brain may be particularly large. Its weight has been evaluated as $\frac{1}{30}$ of the body weight in *Saimiri*; $\frac{1}{48}$ in *Hapale*; and $\frac{1}{45} - \frac{1}{47}$ in *Homo*.

The capucin monkey is famous for its amazing mental alertness, moreover, it should be recalled that both platyrrhines and catarrhines occasionally use some object as a tool.

If such a brain predominance has underlined the early history of Primates, their supremacy over contemporary mammals can readily be understood.

As to the face, the orbital openings are always frontal, the lachrymals and their ducts lying in an intraorbital position. The orbital openings are separated from the temporal fossa by a wide cleft which is present in *Apidium* (Fayoum Oligocene) and still detectable in Man. Among platyrrhines the jugal is prominent in the orbit posterior wall; now, Simons (1972) observes that in *Aegyptopithecus* the bone arrangement "give proof of postorbital closure . . . to about the extent seen typically in the platyrrhine monkeys". Is this not a further indication of the common origin in both platyrrhines and catarrhines? Here we may recall that Ameghino pointed out the presence of a canine fossa in *Homunculus*; this fossa can be detected in Proconsul as well as in a number of other simians and ultimately in *Homo sapiens sapiens*; it is its disappearance in some pongids or a few hominids (notably the classic Neanderthals) that must be envisaged as a secondary character.

Let us now turn to the nasal skeleton. The nasal bones were prominent in *Cebupithecia* (Upper Miocene of Columbia); they are still thus in a wide variety of forms from South America, and do not unite by synostosis, this being a human trait, or do so very tardively. Although platyrrhines stand out because of the lateral position of their nostrils and the broader cartilaginous septum, in some genera at least, the septum is thinner and the nostrils face less sideways (*Aotes*, *Alouatta*).

The mandible displays some plesiomorphic features both in some fossil and living forms. Stress was laid by Hershkovitz (1970) on the parallel evolution of the mandible among platyrrhines and catarrhines. In primitive forms and many modern forms the alveolar rim is narrow and convex anteriorly, teeth are arranged ladder-wise, I_1 anterior to I_2 , the latter to C ; no diastema is present. Such an arrangement, which agrees with that of prosimians and is found among poorly specialized Cynomorphae or fossil pongids,

should be considered primitive and close to the human parabolic curve. By the widening of the incisor region and the tooth array in a straight line, in the upsiloid-shaped platyrrhine mandible (notably in *Alouatta*), as well as in that of a number of other monkeys (e.g. adult pongines), different mandibular mechanics is attained. Worthy of note is the same trend towards enlargement and flattening of the alveolar curve among Australopithecinae and Neanderthals, being a secondary acquisition also in these hominids. The symphysis is slightly retreating (50°) in fossil platyrrhines (*Homunculus*, *Stirtonia*) and in some living form (*Saimiri*: 64°). In *Stirtonia* the symphysis exhibits two human traits, namely, a median eminence at its anterior aspect and a *spina mentalis* at its posterior aspect. In addition, among platyrrhines the simian shelf is consistently absent, so that in most of them, *Homunculus* included, the digastrics are inserted at the posterior aspect of the symphyseal region. In *Homunculus* and several modern forms, the dental closure in side view is seen to follow a curved line (cf. Spee's curve, which is characteristic of Hominids).

All the platyrrhines possess three premolars. Three forms from the Old World, *Amphipithecus* (upper Eocene, Pondaung sands), *Apidium* and *Parapithecus* (Fayoum Oligocene) most often considered to have reached the catarrhinian structural stage [see Szalay (1970) for *Amphipithecus*] also have retained three premolars, yet another feature witnessing the existence of an identical structural phase in platyrrhines and catarrhines. In the three above mentioned forms, as in *Homunculus*, *Stirtonia* and living platyrrhines that are poorly specialized in this respect (*Callicebus*), the dental rows do not exhibit diastemas, the incisors are inserted vertically into their sockets and arranged in *échelon*; the central ones at least, are spatulate, with a horizontal cutting edge. Canines make it possible to distinguish, among Hapalides and Cebides, some forms in which these teeth are large and others in which they are small; generally, sex dimorphism is low. Premolars, slightly molarized, are striking in *Homunculus* and *Stirtonia*, since all three have a single root, this being a plesiomorphic feature *par excellence*, which can be found in *Homo sapiens sapiens*, having disappeared in Australopithecinae on account of the breadth attained by their chewing apparatus. The two distal premolars have the same submolariform structure (cf. the homomorphic premolars in the Hominids).

The enormous interest elicited by both living and fossil platyrrhines lies in their providing a valid picture of an ancestor, also in their immature forms, of all the higher Primates at a very early moment of their history. Several platyrrhine features have been retained among Hominidae. This fact might show that Hominidae, together with Pongidae and Cercopithecidae, were already flourishing when these lineages underwent differentiation. If the Hominidae followed a common path together with the Anthropoids over a long span of time, as immunogenetic and cytogenetic studies seem to suggest (the slight differentiation between the two lineages allowing interfertilization—which might explain the morphological ambiguity of fossils), they succeeded nevertheless in achieving their own evolutionary characteristics, though being protected against a number of restricting specializations.

The higher Primates are likely to have had a very remote common origin, possibly starting from a Euroasiatic prosimian form with a lorisiform otic pattern. The absence of this form among our fossil documents does not prove its non-existence; so far it may not have been discovered or recognized because of its very primitive features. The Primates, reaching Africa at a very remote epoch (upper Cretaceous or Paleocene) would rapidly have become diversified, and a branch, that of platyrrhines, would have

reached the South American continent where, as its history unfolded, many of their plesiomorphic traits would have been preserved, while they developed characters paralleling those of the catarrhines.

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La morphologie du squelette des Platyrrhiniens actuels et fossiles donne souvent l'image de l'ancêtre des Primates supérieurs, homme inclus. Une revue des caractères d'origine communs aux uns et aux autres est établie. Par voie de retour, l'homme actuel s'avère avoir conservé nombreux ces caractères d'origine, ce qui le place sur une lignée évolutive directe et singulière.



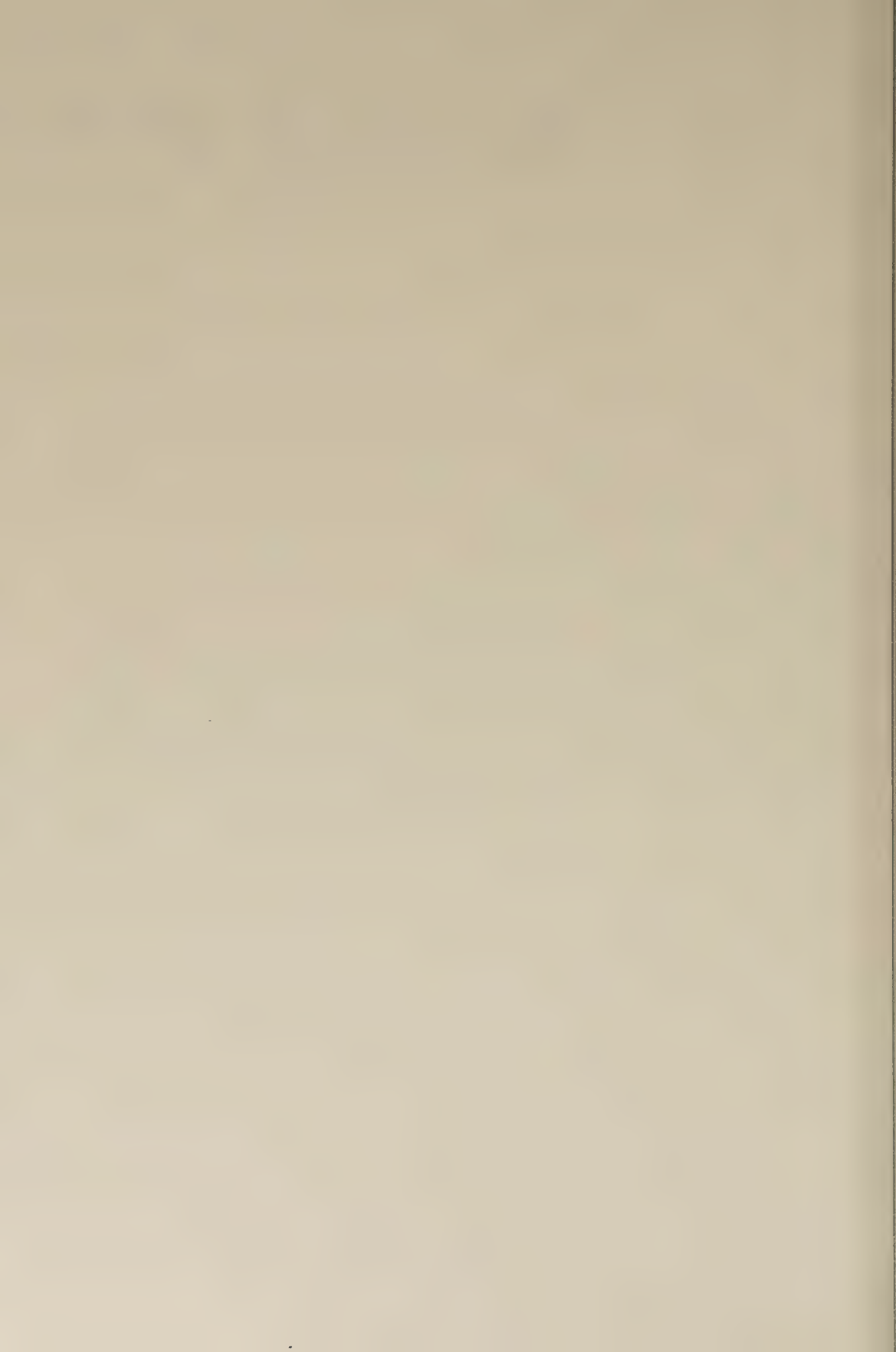
Benjamin Urrutia

University Villa No. 5
Provo, Utah 84601, U.S.A.

Additional Evidence for the Precolumbian Migration of Black African Peoples to the American Continent

Received 3 October 1973

Juan Comas, in a recent article ("Transatlantic Hypothesis on the Peopling of America: Caucasoids and Negroids," *Journal of Human Evolution* 2 (2), 75-92, March 1973) considers, and accepts with little or no reservation, the evidence for Precolumbian (even Paleolithic) Caucasians in North America, and he considers, and rejects, a larger body of evidence for Black Precolumbian migrations. My only complaint (aside from his apparent eagerness to accept the Caucasian data and to reject the Negro data, which may be entirely in the eye of the beholder) is that he considers much of the evidence that is not very solid, but leaves completely untouched a large body of it that seems to be much more convincing than that he does present. Much of it is included in Alexander von Wuthenau's *The Art of Terracotta Pottery in Precolumbian Central and South America* (Crown, 1970). Anthropomorphic figurines, obtained in perfectly respectable excavations, are exhibited, complete with very curly hair, flat noses, thick lips, alveolar prognathism and dark skins. Still more evidence is shown in my review of von Wuthenau's book, in issue 126 (summer 1971) of the *Newsletter and Proceedings of the Society for Early Historical Archaeology* 1971 No. 126 (Summer), (Brigham Young University, Provo, Utah 84601, USA).



Book Review

Physical Anthropology: A Perspective

By John Buettner-Janusch. New York: John Wiley and Sons, Inc. (1973). xiii + 572 pages, appendices, glossary, index. Cloth \$12.00.

To paraphrase the publisher's recent advertisement, it is good to have Buettner-Janusch back again with an updated, streamlined and, in many respects, well-improved text in physical anthropology. Although the author rightly states in his Preface that, despite the obvious similarities between his earlier, more lengthy *Origins of Man* and *Physical Anthropology: A Perspective*, the books were written for different purposes, it is very difficult not to compare them in any review of the present work. Hoping to keep these at a minimum, I will make comparisons when they would appear to illuminate the improvements in the present work.

Physical Anthropology: A Perspective is neatly, and traditionally, divided into two major parts. The first, chapters 1-10, includes presentations of evolutionary theory and concepts, systematics, some functional anatomy, classification and the order Primates, the fossil record and the major features of Primate evolution. The order of presentation of these topics has been changed from *Origins* resulting in a more logical, coherent presentation. This, coupled with a marked reduction in the amount of information presented for some topics (albeit without loss of important conceptual relationships), makes for a text well suited for the undergraduate who might be obtaining his first exposure to physical anthropology.

Following a very brief introduction to the scope of physical anthropology as he sees it, Buettner-Janusch begins with a discussion of the terms and concepts of the modern synthetic theory of evolution, dating techniques, and systematics. The chapter on systematics presents well the difficulties of applying biological concepts, for the most part based on living organisms, to the evidence presented in the fossil record. The problems of species definitions and speciation have been clarified greatly and these concepts are continually brought up when the discussion turns to interpretation of the fossil material.

Before beginning the order Primates and the fossil record, the author lays some groundwork in his chapter on functional anatomy, including a nice presentation of variations of cranial morphology both within and between Primate species. The inclusion of this

chapter before the Primates improves the logical reading of the text and makes more understandable the subsequent classification, characteristics and trends of the Primates in their evolutionary perspective. His *caveat* to the student not to become overwhelmed by the details of his chapter on teeth, bones and muscles, may fall on deaf (or numbed) ears. Marked improvement here might have been obtained by simplifying the illustrations of the skeletal musculature and including visual demonstrations of the limb, head and trunk movements which are merely talked about or listed in charts.

The chapter on the living Primates represents a condensation of the original eight and has been markedly improved visually with the inclusion of many new and better illustrations of representatives of all the major taxa. For comparative purposes, though, it would have been nice to have seen an insectivore.

The chapter on pre-Pleistocene fossil Primate material is notable for its generally well-illustrated format of the major forms representative of each geologic epoch. Students might wonder what *Rooneyia viejaensis* (p. 126) really is, for the author never mentions this fossil in text, glossary or index, although it is listed in Appendix I. A very confusing aspect of this chapter is his use of the common term 'dryopithecine group' which he states includes two subfamilies of the Pongidae, the Gigantopithecinae and the Dryopithecinae, and *Ramapithecus* of the Hominidae. If one must use a generic, in the broad sense of the word, to include all members of a taxonomic group, then its use should be limited to the inclusion only of those members which belong to the taxon from which the generic term was derived. I assume Buettner-Janusch is using this term to reflect the systematic relationship he discusses later. Here the 'dryopithecine lineage' is seen as splitting in the Miocene or earlier into the pongids, on one hand, and the hominids as *Ramapithecus* on the other. If, then he views the dryopithecine lineage as being ancestral to both pongids and hominids his taxonomy should reflect this relationship. It does not. The two alternative classifications he presents (pp. 263-264) places the Dryopithecinae as a subfamily of the Pongidae, and the Hominidae as a family of equivalent taxonomic rank with the Pongidae. If the dryopithecine lineage as he sees it gave rise to pongids and hominids, then the taxa should reflect this by elevating the dryopithecine group to superfamily rank or reducing pongids and hominids to the rank of tribes. This whole discussion, though, could have been easily avoided had the author not been so lax in his use of the generic 'dryopithecine.' I am afraid this will cause undue confusion for the average student who tries to figure out just who gave rise to whom.

As a beautiful discourse of the logical process that one man has gone through in making an assessment of the Pleistocene hominid material, Buettner-Janusch's chapter on the systematics of the Hominoidea will be a highlight of the book. The classroom teacher, however, will certainly have to make clear the author's conclusions are not as widely accepted as he might lead one to believe, particularly the loss of *Homo erectus* as a valid taxon.

The second part of the book, chapters 11-16, is virtually unchanged from *Origins* except in reduction of words and new and better illustrations. It includes good discussions of basic human and molecular genetics, blood group and biochemical variations, very little on race, and the author's view of whither mankind. It is curious, too, that this part contains the only passing reference to the role of biochemical analysis in the attempt to clarify some of the problems of the fossil record. The work of Sarich, Wilson and others in this area, although highly controversial, is not even mentioned or referenced. This is disturbing because Buettner-Janusch in many areas has not shied away from

controversy and has presented some well-balanced discussions throughout the book. This is a glaring, almost obvious, omission.

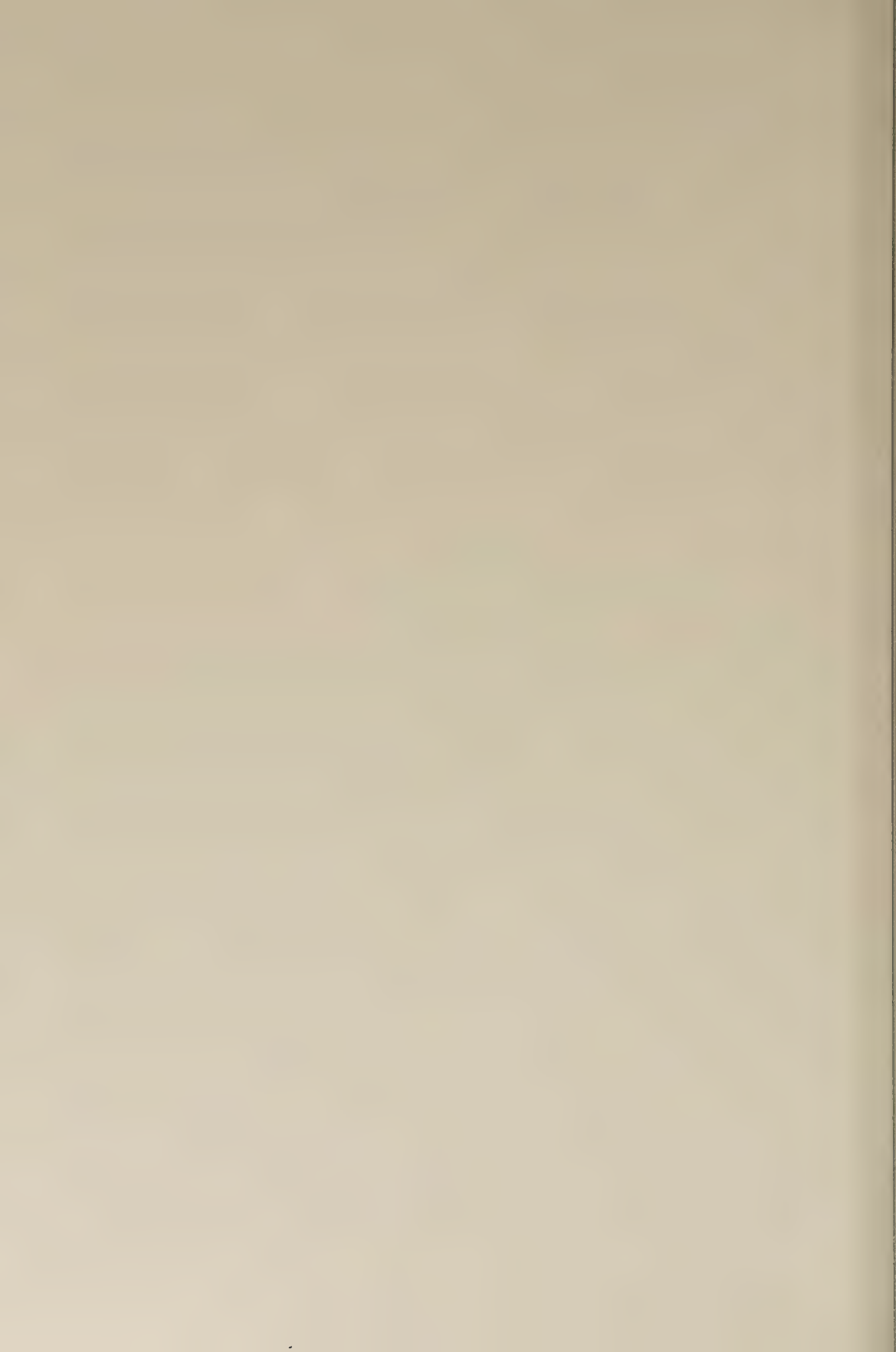
This second part of the book I can sum up as having, for my particular tastes, too many molecules and not enough traditional physical anthropology which still has much to say to us. But since the book is subtitled *A Perspective* I suppose this is fair enough.

Another weakness in the book as a whole is the separate Credit List buried in the back of the book rather than with the illustrations themselves. This is lazy editing and serves to reduce the stimulus to the student to pursue an outside source on his own. Strengths include excellent appendices, untitled in the Table of Contents, on taxonomic relationships of numerous fossil Primates, complete definitions of members of the Hominoidea by several authors, and synonymies of names of the Hominidae; a good glossary; and well-presented index.

In short, Buettner-Janusch has done an excellent job of trimming *Origins* to an efficient size which I look forward to using in the classroom. I cannot help feeling, though, that *Physical Anthropology: A Perspective* represents more editorial deletion of *Origins of Man* than a new and 'different' book. But the deletions have brought the ideas of an eminent scholar to a level which the beginning undergraduate should readily appreciate.

J. MICHAEL HOFFMAN

*Department of Anthropology,
Northern Arizona University,
Flagstaff, AZ 86001
U.S.A.*



Journal of Human Evolution

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1. *Journal of Human Evolution* will publish papers dealing with the evolution of Non-human Primates and the natural history of Man. The main purpose of this periodical is the collection in a unique journal and the prompt publication of original articles dealing with data and facts concerning the physical and sociological evolution of Non-human Primates and the origin and evolution of Man. The *Journal* will not as a rule publish papers when the subject matter is outside the fields defined above; however, when the subject matter borders on general problems of vertebrate evolution such papers may be published when space permits.

The *Journal* will also publish Letters to the Editor (averaging 1000 words) and comprehensive reviews of books and papers, bibliography of current publications, abstracts and informal communications on the same subject.

The *Journal* has to be published in English as this is the most widespread language in scientific literature; however, no geographical or ideological restriction will be imposed on the contents by the editors. Papers should contain the maximum density of information compatible with clarity, and every sentence should be scrutinized to ensure that its presence is essential. *Careful preparation of manuscripts will aid prompt publication; carelessness will cause delay.*

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(a) *Summaries.* An abstract will be printed at the head of all papers, including Letters to the Editor; this should generally not exceed 300 words, and should be intelligible to the general reader without reference to the main text. Abbreviations should be avoided. As well as the summary in English, authors may submit a summary in their usual language, the length not to exceed 300 words.

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Line drawings will be referred to as Figure 1, Figure 2, etc., and photographs as Plate 1, Plate 2, etc. The name(s) of the author(s) and the number should be written on all illustrations, together with the indication "Top" if necessary. Besides the original illustrations one duplicate set must accompany the typescript: these may be photo-prints and need not be of the same quality as the originals, but they must be clear and legible. If greatly oversize original drawings are submitted they must be accompanied by two sets of smaller photo-prints.

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Continental Drift, The Rift Valleys and the Origin of the Different Stock of Primates

During the last decade extensive investigation in marine geology rejuvenated Wegener's hypothesis that the continents had drifted apart from a single "Panagea" and data are provided in support of a still relatively recent connection between Africa and South America. This evidence will open the possibility that at least some of the Primate groups existing in South America could be derived from ancestors who directly arrived in South America from Africa. This possibility is in contrast with the traditional theory which instead assumes that all the Primates of South America are derived from a Prosimian group originally inhabiting North America (Omomidae).

An extension of this concept for other land masses can contribute to solving the problem of the origin of other stock of Primates.

In a series of forthcoming requested papers and contributions the Editor is trying to collect relevant information on the possible origins and correlations of the different stocks of Primates starting from the South American one.

Different anatomical, paleontological, biochemical, cytogenetical and zoogeographical aspects will be considered. Some contributions on this topic have already been published in previous issues, others will follow.

This effort has been possible thanks to an award of the University of Toronto, Humanities and Social Sciences Grant 1973-74.



H. Lamendin

*Institut de Biologie Appliquée au
Domaine de la Santé,
Université d'Orléans, France*

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Observation with SEM of Rehydrated Mummy Teeth

SEM observation of Egyptian mummy teeth progressively rehydrated shows the perfect conservation of their tissues. This fact amongst others permits one to introduce a new parameter using SEM to estimate the age of mummies. Structural similarity between observed teeth which are of various dates must be outlined. What is the real importance of 4000 years in the world's history?

1. Introduction

During researches on teeth of various epochs, we have been able to observe, for the first time in 3 dimensions, due to use of SEM, the globular mineralised structures of the circum-pulpar dentine, on prehistoric specimens. We observed them later on, on contemporary teeth, treated by calcination (Lamendin, 1972*b*). They can be seen too after treatment by sodium hypochlorite (Kerebel, 1971).

In neolithic teeth, which have remained buried for a long time in a calcareous soil (Horemas, 1965) the globules are completely free. In prehistoric teeth belonging to mummies, which were almost of the same period (with a difference of about 500 years) these globules were less free. It is about these mummy teeth that the present work is concerned. Anyhow, some general points have to be considered first.

2. General Points

If we refer to etymology, the word mummy (in low Latin, *mumia*; in Arabic, *moumya*; in Iranian, *moum*, which means wax) is applied to embalmed bodies. By extension, it also concerns bodies dried naturally and preserved under the influence of dry and warm air and depending on the nature of the soil. Generally, sandy soils are favourable to this preservation. Evidently, protection against humidity, and absence of humidity and of various insects are necessary. All things considered, mummification means the desiccation of the tissues enabling them to resist putrefaction,* which is, as we shall see, confirmed once again here. Maybe, because of their state of preservation therapeutic properties have been attributed to mummies in Europe when the first crusades came back to Europe. We must note that, in Ancient Egypt, this desiccation was sometimes obtained in an oven, the corpse being either immersed for a while in melted wax and/or treated, internally and externally, by various techniques using aromates, balsams, antiseptics, varnishes, pitch, gums, etc. This possibility corresponds to the first meaning of the word mummy which is associated with that of embalming.

* *Dictionnaire encyclopédique Quillet*, Paris, p. 4336.

3. Material and Methods

The teeth studied here originate from mummies of the "common class", dried naturally (excavations made by G. Marro in High Egypt; sites Gebelen and Asswan). We obtained them thanks to B. Chiarelli and M. Masali (Istituto di Antropologia, Turin, Italy). Their date is about 3500 B.C., i.e. by the end of the Middle Empire.

In a first set of trials, dry fragments of these teeth were observed using a scanning electronic microscope (SEM) (JEOL.JSM U 3 at BRGM-CNRS-Orléans, France), then, in a second step, they were observed after progressive rehydration. This rehydration, lasting one week, was made by immersing the fragments successively in alcoholic solutions of decreasing strength (95, 75, 55, 35 and 15%) diluted with sterile isotonic solutions of sodium chloride (9/1000) during 24 hr for each solution, placing them finally in isotonic sodium chloride in which they remained for 48 hr, before the examination. For comparison some photographs concerning neolithic (Eteauville ossuary. Lutz-en-Dunois, France, Nouel *et al.*, 1965) and contemporary (Bourges and Orléans, France) teeth are presented here (Lamendin, 1972a, b, c).

4. Observations

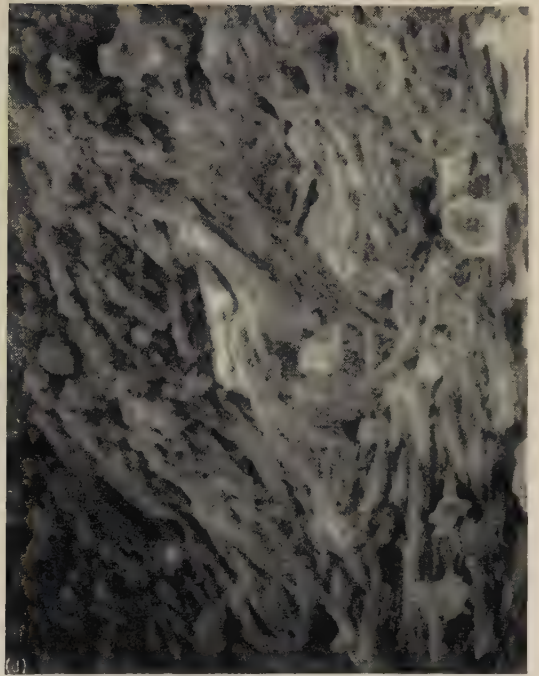
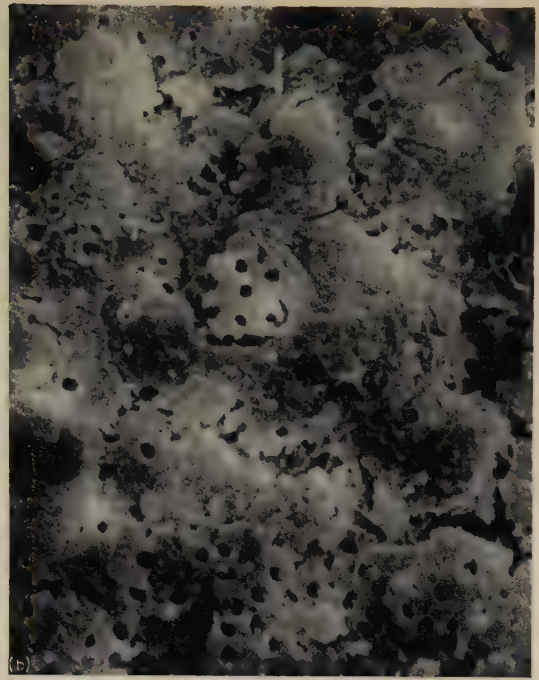
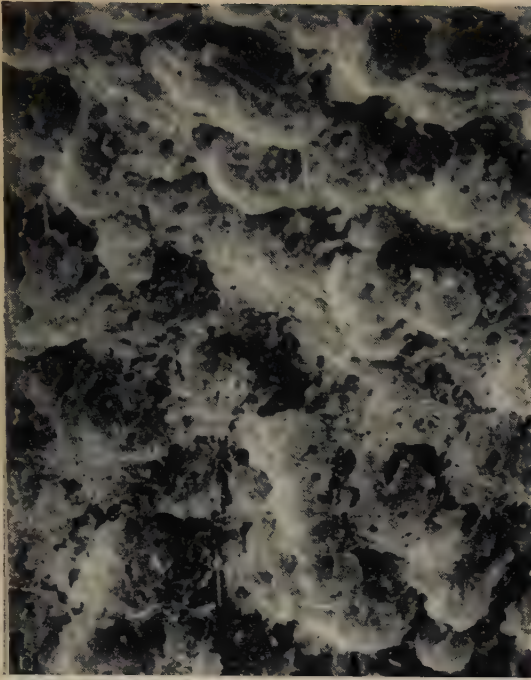
Examination of the circumpulpar wall in a non-rehydrated tooth shows on one side a smooth aspect [Plate 1(a)], and on the other side a highly desiccated aspect [Plate 1(b, c)]. On a rehydrated fragment of the same tooth [Plate 1(d)] two zones can be distinctly observed: one, to the left [Plate 2(a)] is clear, the other to the right [Plate 2(b)] is covered with pulpal remnants. This difference may be caused either by desiccation or fracture of the tooth.

On a longitudinal fracture, at the level of dentinal tubuli of a non-rehydrated fragment, the observed picture [Plate 3(a)] may be thought to be caused by contamination and the hair-like aspect of the collagen fibres is characteristic [Plate 3(b)]. On a rehydrated fragment, the pictures [Plate 3(c, d)] observed are very different and can be considered as normal.

Plate 4(a) concerns the edge of the root canal in a rehydrated fragment, in a "no longer inhabited zone". Dentinal tubuli can be seen transversally broken (top left of the picture) and longitudinally broken near the centre. They reach the mineralized globules (bottom). Plate 4(b) underlines the same fact and can be compared with Plate 4(c) showing the same "inhabited zone" on a contemporary tooth.

Plate 5(a) shows clearly one of the dentinal globules, almost in profile, which can be compared with Plate 1(c) (non-rehydrated tooth) and especially with Plate 5(b) showing a calcinated contemporary tooth. Concerning this fact it can be noted that, generally speaking, the mineralized globules seem bulkier at the coronary level than at the radicular level.

It is possible to compare: (i) Plate 2(a) with Plate 5(c) concerning a neolithic dry tooth; (ii) Plate 2(b) with Plate 6(a-c) showing the various aspects of the wall of the pulpar cavity of contemporary teeth of a 71 year old individual [Plate 6(a)] and 29 year old man [Plate 6(b, c)]; (iii) Plate 3(d) with Plate 7(a) where the internal peripheral tunique of collagen fibres offers the same aspect as in the figure obtained of a fracture of a dentinal on a contemporary tooth; (iv) Plate 7(b) obtained on a fragment of a rehydrated mummy tooth with a contemporary tooth where an odontoblastic process can



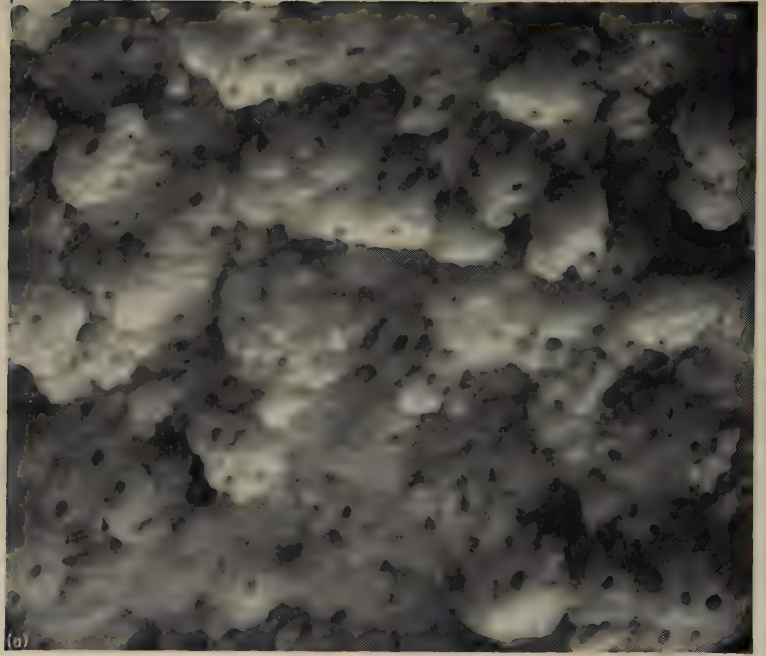
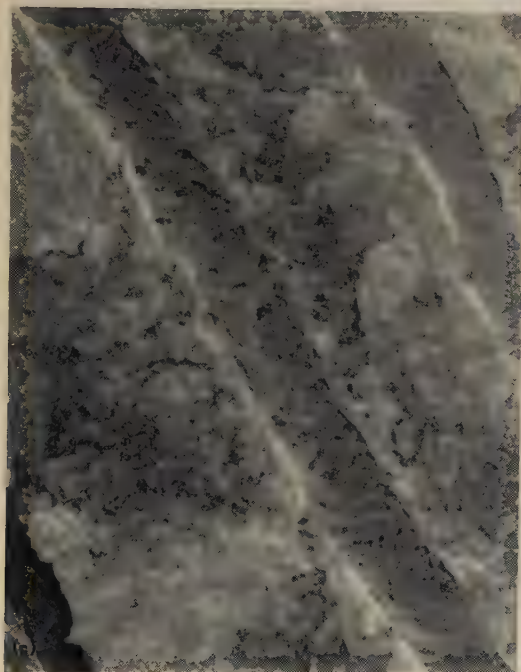
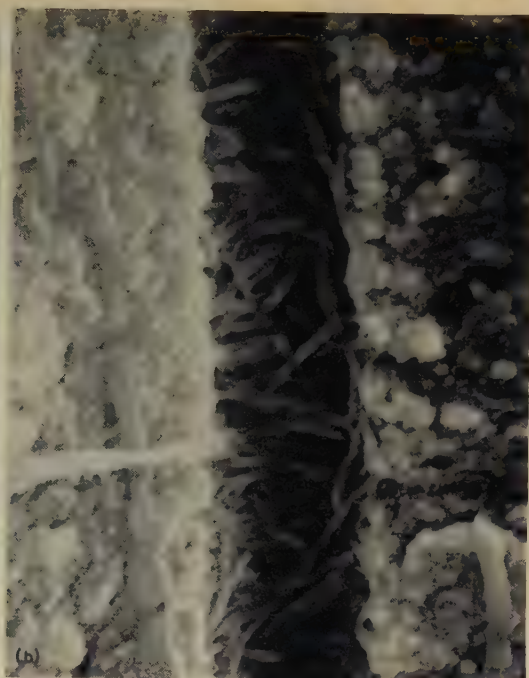
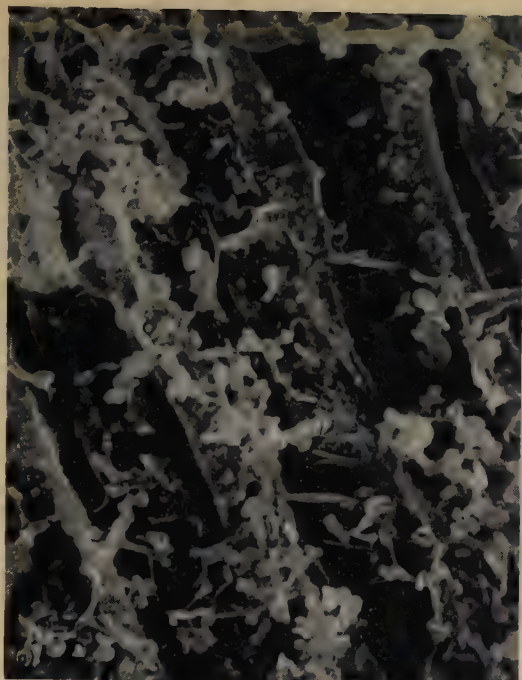


Plate 3. (a) $\times 3,000$, (b) $\times 9,000$, (c) $\times 3,800$, (d) $\times 10,000$.



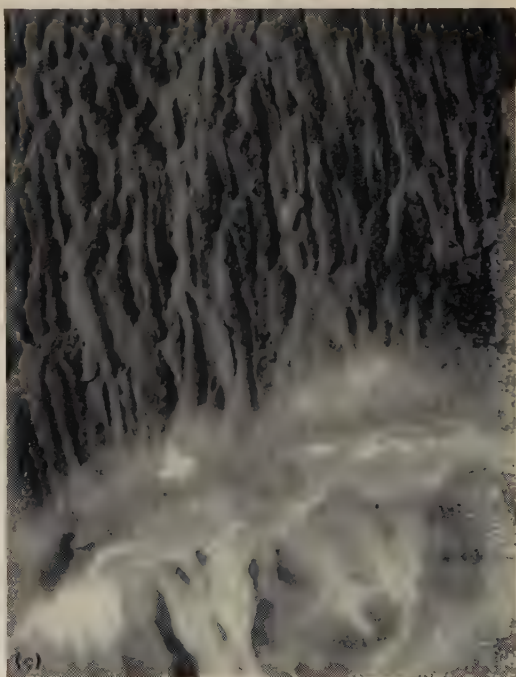
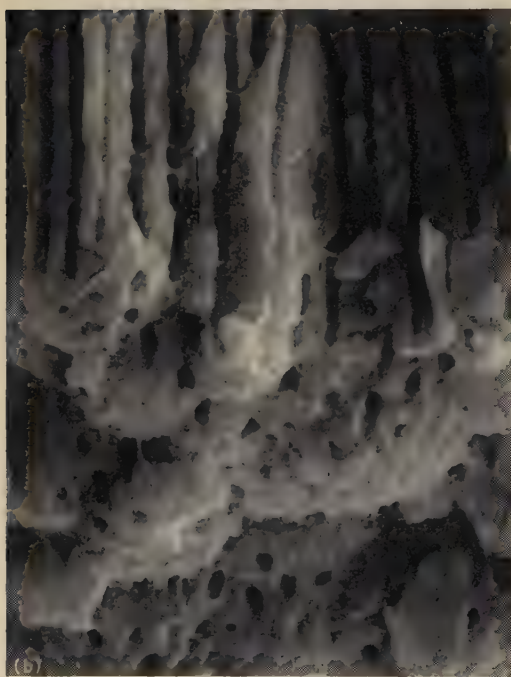
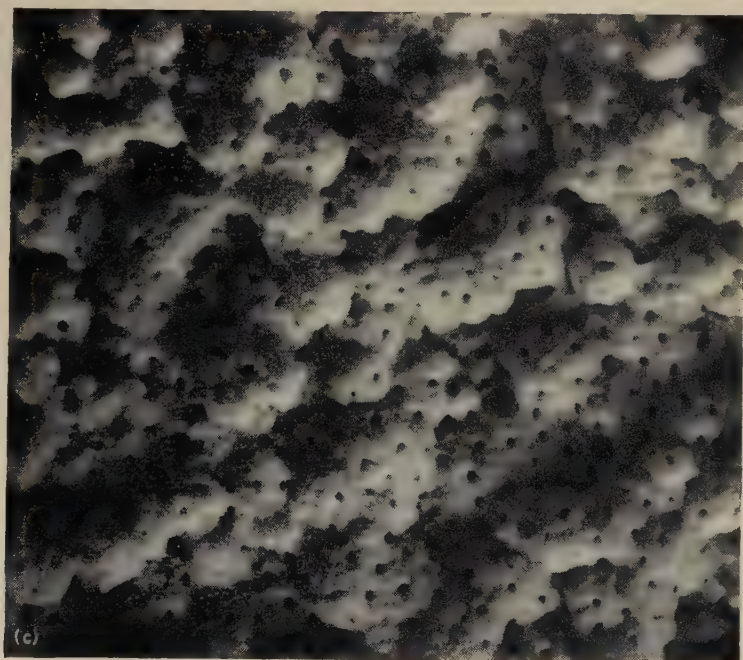
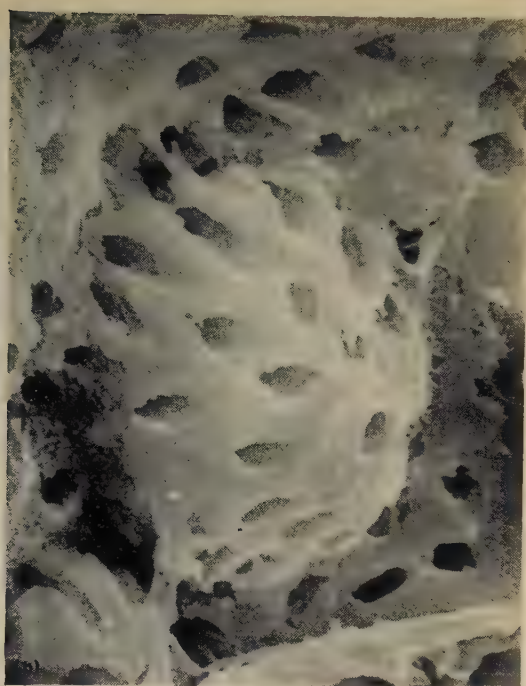
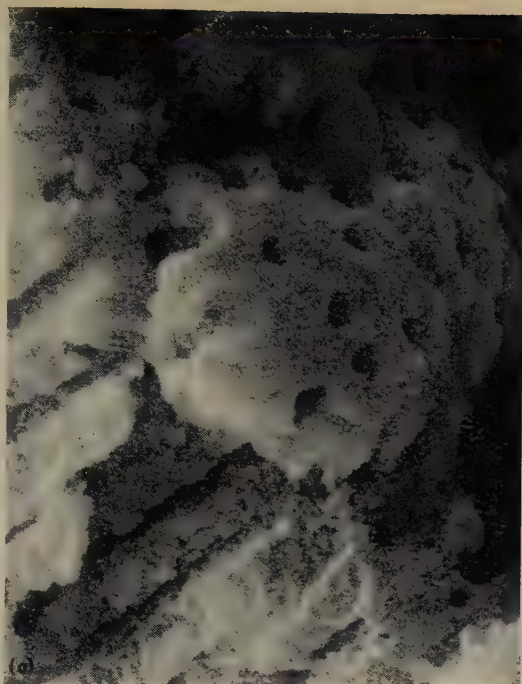
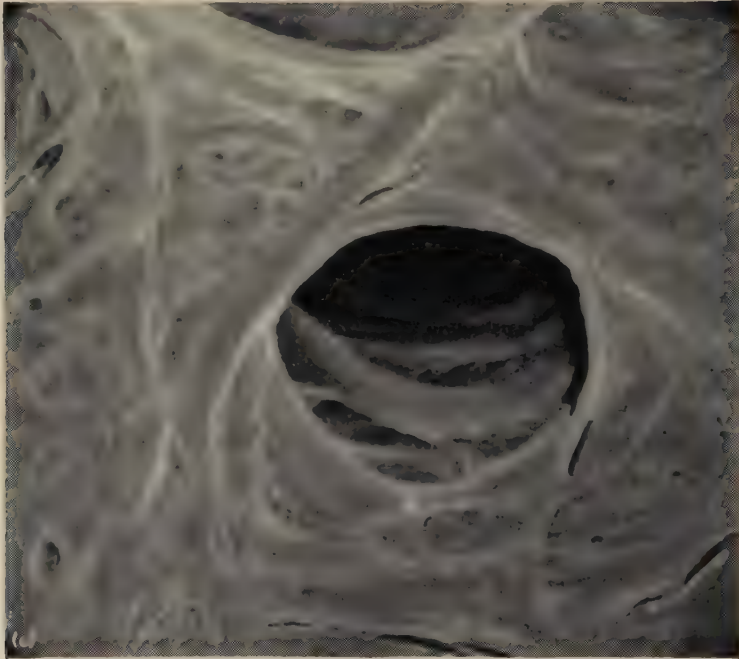
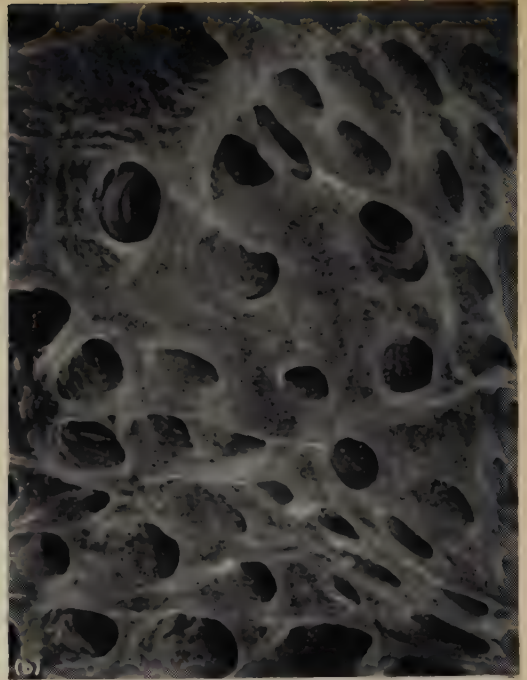
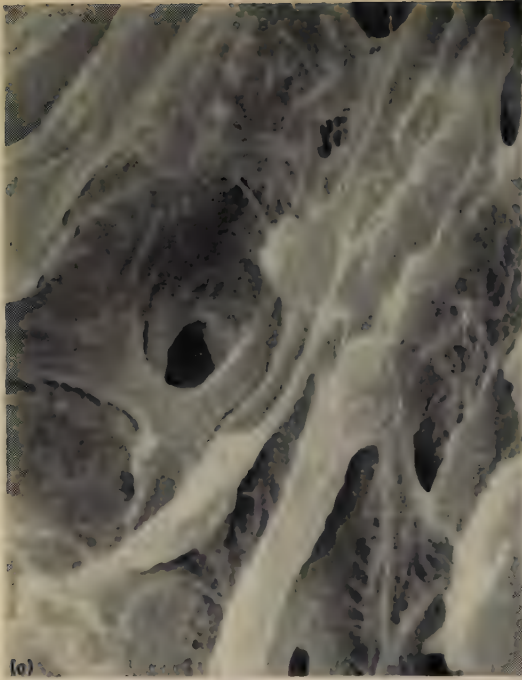
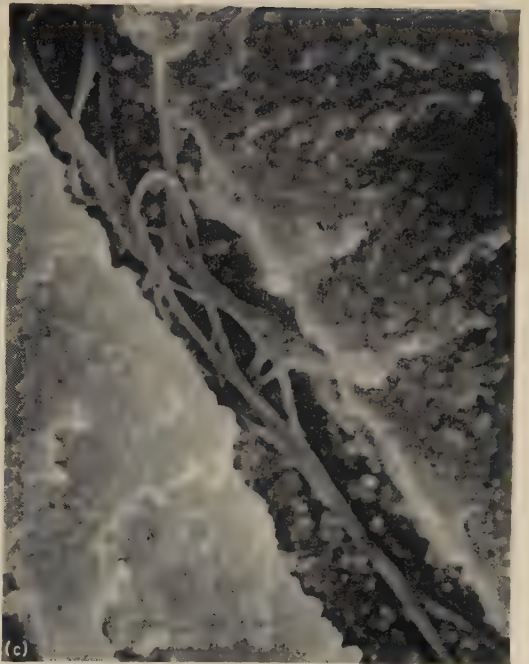
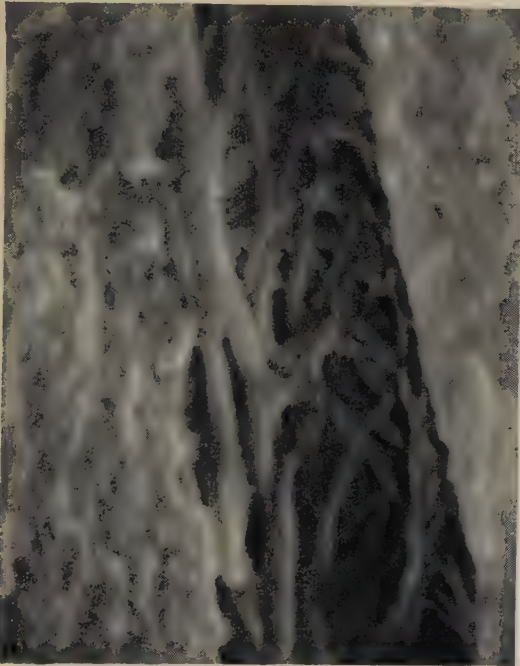


Plate 5. (a) $\times 2,000$, (b) $\times 3,000$, (c) $\times 600$.









be observed showing convergencies, divergencies and even a loop [Plate 7(c)]. Plate 7(b) (left) could be interpreted as an odontoblastic process seen on a wall of collagen fibre whereas the details of Plate 7(c) are seen on a granularly wall.

Note

In Plate 7(c) the intertubulinal space is not as strongly granulated as the tubular wall, contrary to a case published by Nief (1973) concerning the tooth of an aged man (71 years old), tooth undergoing a process of natural demineralization. On fossil teeth, in good state of conservation, organic residues have been shown by Lavergne *et al.* (1969).

5. Discussion and Conclusion

Rehydration of various mummified tissues is well known. For instance the rehydration of red blood cells has been published by Chiarelli & Rabino Massa (1967). Anyhow, our method differs from theirs which uses 95% alcohol, a slightly formulated solution and a third solution containing sodium carbonate (Sandison, 1955) at a constant alcoholic concentration. As our aim is not to prepare paraffin embedding but to obtain a directly observable preparation, the two methods cannot be compared.

The method used by us gives a conclusive response which specially underlines the perfect conservation of predominately organic tissues in the studied teeth.

The SEM allows various and precise observations which obviously show the similarity of structures of teeth of various dates. We will note more specially the structures of dentinal tubuli and of their content on which we have done much work elsewhere. One of the SEM applications is a new test possibly usable for age estimation (Lamendin, 1972*c*, 1973).

Studying again the tubuli walls visible on Plates 7(b) and 7(c), we have noted that the second was granular. The disappearance of the peripheric internal sheet of collagen fibres is in fact partly related to the aging of the organ (which does not mean aging of the general system). Plate 7(c) concerns a 67 year old person. The lack of collagen fibres may also originate from other factors, for instance pathological ones, or more simply from the disappearance of organic compounds in general by chemical action calcination or fossilization. Plates 3(c) and 7(a), as we have already mentioned, present some similarities and the last one shows a tooth belonging to a 25 years old person.

These figures concern only two typical examples, but the approach of age estimation by SEM needs more observations. Accordingly we are carrying on this work.

At the end of our research we asked Masali if he had, by his own methods, estimated the age of the mummies on which the samples examined have been taken. We received figures which corroborated our opinion. It is true that his estimations were more precise than ours but they had been obtained with more elements than a single tooth.

Table 1

Mummy tooth	Author estimation	Masali's estimation
No. 14684	Adult young	30-35 years
No. 416	Very young adult or big adolescent	18-20 years

According to Lengyel (1964), "It is extremely interesting either for the anthropologist or for the stomatologist who study this science to know as precisely as possible the exact age of the death of the subject whose bones or teeth he is studying. Numerous methods have been proposed for this aim. None of them gives satisfactory results in every case".

This is our opinion too.

We thank Mr Jeanrot of the Bureau de Recherches Géologiques et Minières et Mr Nief for their help. This work has been carried out in the Laboratoire de Biologie Cellulaire et Animale de la Faculté des Sciences d'Orléans (Prof. R. Delavault).

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La réhydratation progressive de dents de momies égyptiennes et leur observation au M.E.B. met en évidence la parfaite conservation de leurs tissus. Celle-ci permet, entre autre, d'introduire à propos de l'estimation d'âge des momies un critère nouveau découlant de l'emploi du M.E.B. Enfin la similitude des structures présentées par les dents de diverses datations, examinées, est à souligner. Que sont, il est vrai, 4000 ans dans l'histoire du monde!

Laboratory of Medical Genetics,
University of S. Paulo, Brazil

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Karyotypic studies were carried out on some species belonging to the family Cebidae. The chromosome complements have been studied in blood cultures *in vitro* in the following species: *Alouatta fusca clamitans* ($2n = 50$); *Aotes trivirgatus* ($2n = 52$); *Cebus albifrons* ($2n = 52$); *Cebus* sp. ($2n = 54$); *Ateles paniscus paniscus* ($2n = 34$); *Lagothrix lagotricha* ($2n = 62$). Comparison between the present results and the karyotypes of the Cebidae described in the literature reveal intra-specific and interspecific variability in number and structure of the chromosomes.

1. Introduction

Karyological data concerning the genus *Alouatta* have been reported only for the following species: *Alouatta seniculus* with 44 chromosomes in the diploid complement (Bender & Chu, 1963); *Alouatta villosa* with 53 chromosomes (Hsu, 1965) and *Alouatta caraya* with 52 chromosomes (Egozcue & Egozcue, 1966a). The diploid complement of *Aotes trivirgatus* was described with either 54 or 50 chromosomes (Chiarelli, 1961; Chiarelli & Barberis, 1966), while Brumback *et al.* (1971) reported karyotypes with 54, 53 and 52 chromosomes in *Aotes trivirgatus griseimembra*.

Constancy in the diploid chromosome number in the genus *Ateles* has been reported in all species dealt with in the literature. *Ateles arachnoides* and *Ateles paniscus* have 34 chromosomes, but no information on their karyotypes is available (Chiarelli, in Chu & Bender, 1962; Chiarelli, 1961). *Ateles paniscus chamek* has 34 chromosomes with 6 metacentric, 9 submetacentric and 1 acrocentric pairs, while the X chromosome is metacentric and the Y acrocentric (Bender & Mettler, 1958). *Ateles belzebuth* (Chu & Bender, 1961) and *Ateles geoffroyi cucullatus* (Bender & Mettler, 1958) have identical karyotypes with 34 chromosomes, including 3 metacentric, 9 submetacentric and 1 acrocentric pairs, a metacentric X chromosome and an acrocentric Y. According to Egozcue & Hagemenas (1967), the X chromosome of *Ateles geoffroyi cucullatus* is submetacentric, the Y either acrocentric or submetacentric. The X and Y chromosomes of *Ateles geoffroyi* were described as metacentric by Hsu & Benirschke (1968) and by Egozcue *et al.* (1969).

The karyotype of *Lagothrix uericola* was described by Bender & Chu (1963) with 62 chromosomes, and that of *Lagothrix lagotricha* was recorded from a female specimen with 32 submetacentric and 30 acrocentric chromosomes by Egozcue & Perkins (1970).

Cebus capucinus was described with 52 (Egozcue & Egozcue, 1966b) and 54 chromosomes (Bender & Mettler, 1958; Egozcue, 1969). The X chromosome was reported to be either submetacentric or acrocentric and the Y to be acrocentric. *Cebus albifrons* was reported with 54 chromosomes including 3 metacentric, 7 submetacentric and 16 acrocentric pairs in the diploid complement; the X chromosome was submetacentric and the Y acrocentric (Egozcue & Egozcue, 1967). *Cebus apella* had 54 chromosomes with 3 metacentric, 9 submetacentric and 14 acrocentric pairs in the complement; the X and Y chromosomes were acrocentric (Bender & Mettler, 1958).

Karyological studies on the species of the family *Cebidae* seem therefore to show an appreciable intraspecific and interspecific variability in their chromosome number. The numerical and structural changes undergone by the chromosomes belonging to representatives of that family may provide some clues for understanding the phylogenetic relationships among the New World Primates.

The purpose of this paper is to report our own data on the above mentioned and other species of *Cebidae* in an attempt to establish a karyological relationship among this group of Primates.

2. Material and Methods

The six individuals of *Alouatta fusca clamitans* ("bugio ruivo" or "guariba") investigated here were captured in the neighbourhood of the Horto Florestal da Cantareira, State of São Paulo, Brazil. The male specimen of *Aotes trivirgatus*, the male and the female of *Ateles paniscus paniscus* ("macaco aranha" or "coatá de cara vermelha"), the male classified as *Lagothrix lagotricha* ("macaco barrigudo"), the male and the female of *Cebus albifrons* ("macaco caiarara") and the unidentified *Cebus* sp. ("macaco prego") all belong to the São Paulo Zoo, Brazil.

Chromosome study was carried out according to a modified technique based on Moorhead *et al.* (1960): 0.1 ml Heparinized blood obtained by venipuncture was incubated in Hanks saline (60 %) supplemented with 20 % of a 2.5 % lactoalbumin hydrolysate solution, 20 % inactivated calf serum, 0.5 % Phytoclin (Wellcome), 0.001 % glucose and antibiotics (Penicillin and Streptomycin).

Cultures were incubated for 72 to 96 hr and treated with colchicine (0.04 ml of a 4×10^{-5} M solution); after 2 or 3 hr, 4 ml of a hypotonic solution (0.17 % NaCl) were added; the slides were prepared by the air drying method and stained with Giemsa (QEEL).

Photomicrographs were taken on Recordak Microfile Kodak film, and the karyotypes were prepared from the enlarged photographs. The chromosomes were paired and arranged in order of decreasing size. Appropriate metaphase plates were used for measuring the chromosomes.

Chromosome length was calculated as percentage of the total X-containing haploid complement length (% TCL). Average values based on 4 metaphase plates from the same specimens were obtained for each chromosome pair.

3. Results

Table 1 shows the distribution of chromosome counts and diploid numbers of the different animals studied.

Alouatta fusca clamitans exhibited 50 chromosomes with 2 metacentric, 8 submetacentric and 14 acrocentric pairs in its diploid complement. The X chromosome was a medium sized submetacentric and the Y a small acrocentric chromosome. At least three acrocentric pairs showed a deep secondary constriction in the long arm [Plate 1(a, b)]. Two males of *A. fusca clamitans* showed 49 chromosomes in the diploid complement. It is likely that aneuploidy was due to the loss of a small acrocentric chromosome.

Aotes trivirgatus shows 52 chromosomes with 3 metacentric, 8 submetacentric and 14 acrocentric pairs; the X chromosome was metacentric and the Y was a small acrocentric. A deep secondary constriction was also seen in one metacentric pair (pair J) [Plate 1(c)].

Plate 1. (a) Karyotype of *Alouatta fusca clamitans* (male), and Karyotype of *A. fusca clamitans* (male with 49 chromosomes), (b) Karyotype of *Alouatta fusca clamitans* (female), (c) Karyotype of *Aotes trivirgatus* (male), (d) Karyotype of *Lagothrix lagotricha* (male).

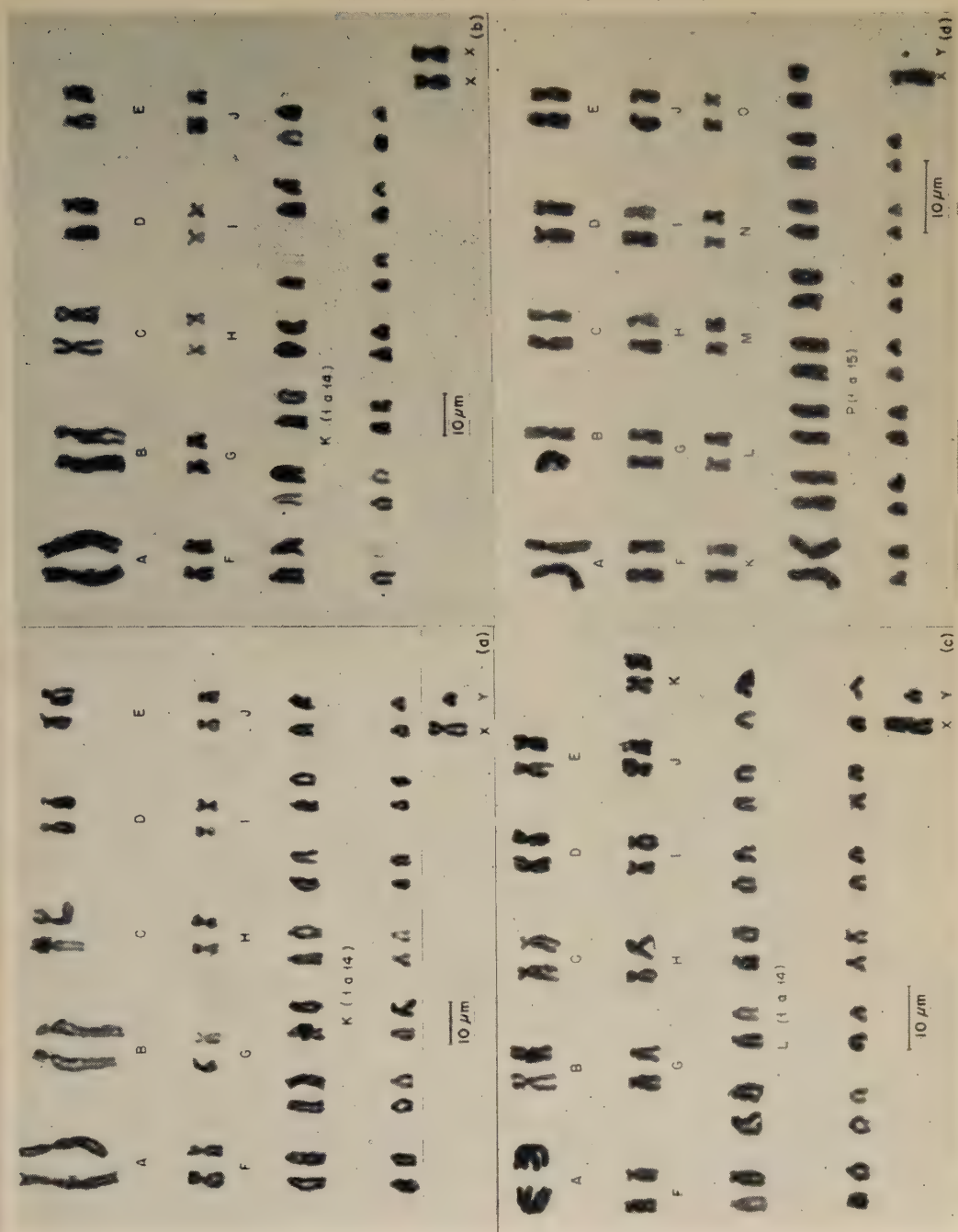


Plate 2. (a) Karyotype of *Ateles paniscus paniscus* (male), (b) Karyotype of *Ateles paniscus paniscus* (female).

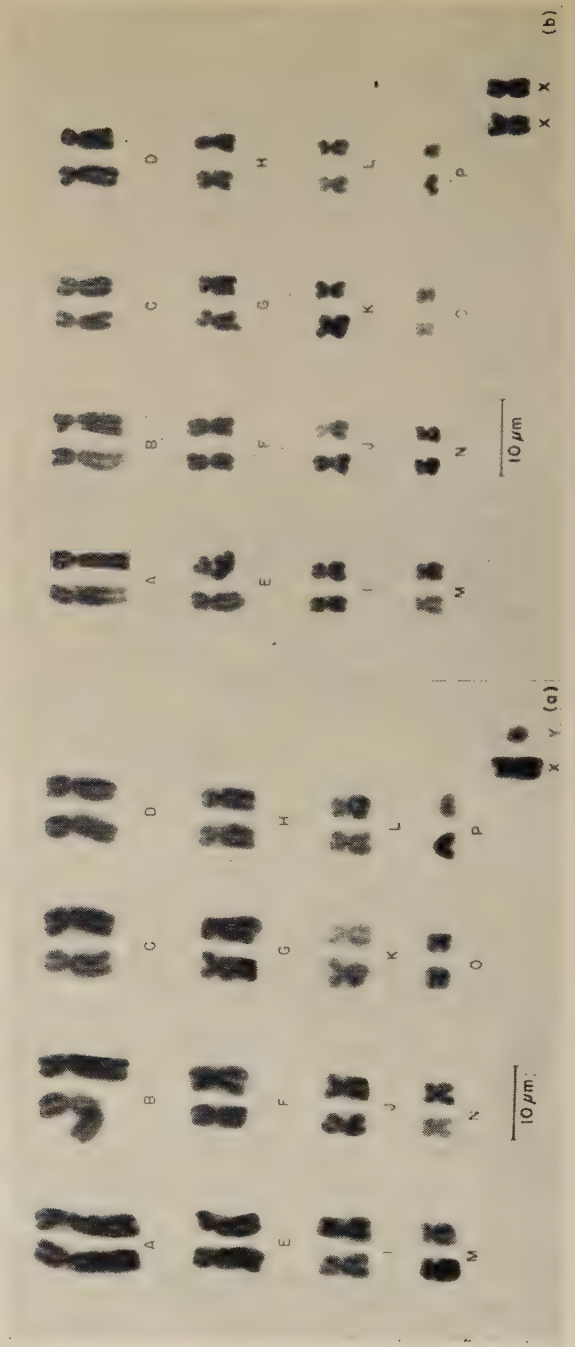


Plate 3. (a) Karyotype of *Cebus albifrons* (male), (b) Karyotype of *Cebus albifrons* (female), (c) Karyotype of *Cebus* sp. (male), (d) Karyotype of *Cebus* sp. (female).

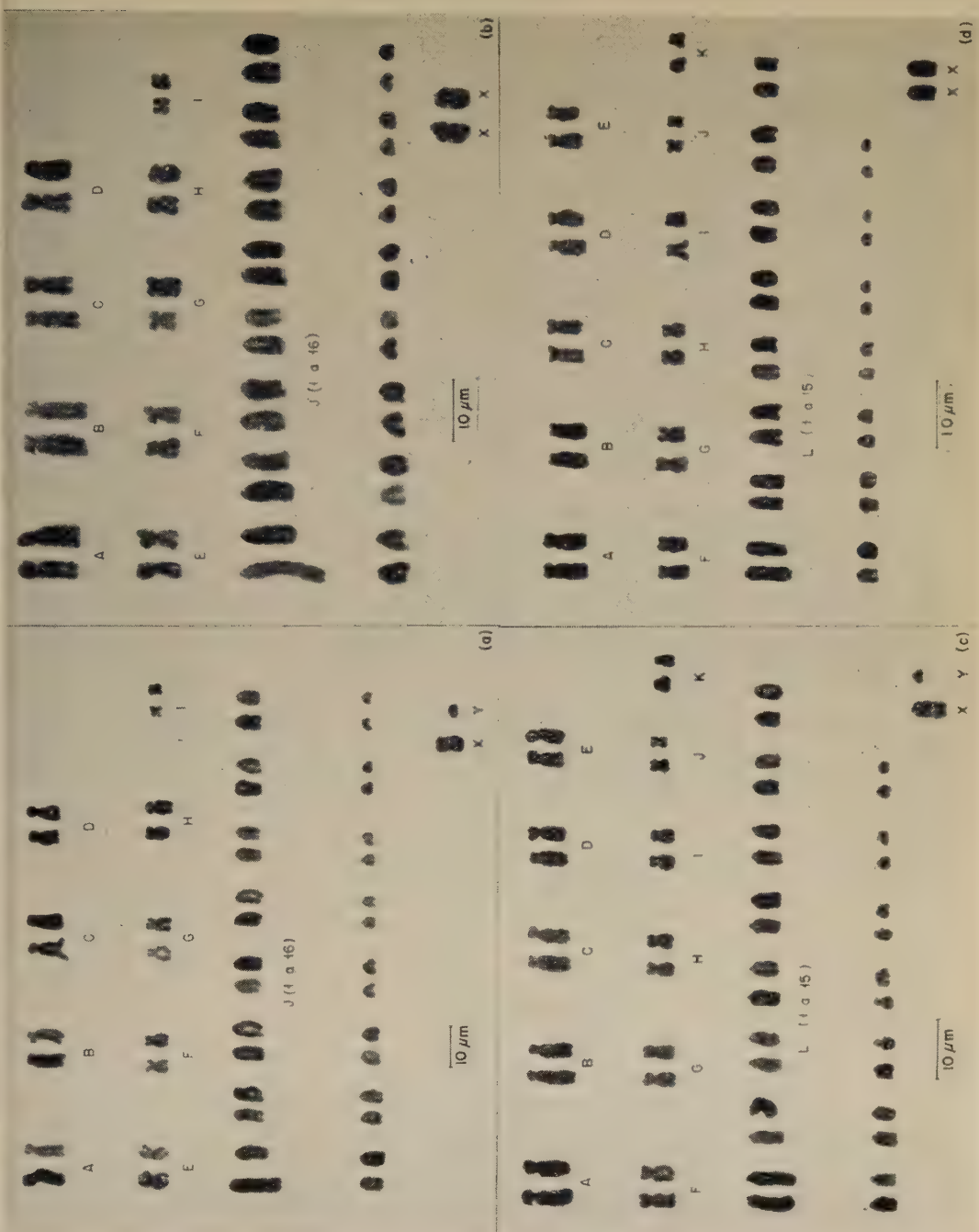




Table 1

Distribution of chromosome counts and diploid number (2n) of the species studied

Species	Sex	Number mitoses studied	Chromosome number												Diploid number
			33	34	48	49	50	51	52	53	54	61	62		
<i>Alouatta fusca clamitans</i>	♀	12	—	—	—	—	12	—	—	—	—	—	—	50	
<i>Alouatta fusca clamitans</i>	♀	7	—	—	—	—	7	—	—	—	—	—	—	50	
<i>Alouatta fusca clamitans</i>	♂	10	—	—	—	1	9	—	—	—	—	—	—	50	
<i>Alouatta fusca clamitans</i>	♂	5	—	—	—	1	4	—	—	—	—	—	—	50	
<i>Alouatta fusca clamitans</i>	♂	10	—	—	—	1	9	—	—	—	—	—	—	49	
<i>Alouatta fusca clamitans</i>	♂	12	—	—	—	1	11	—	—	—	—	—	—	49	
<i>Ateles paniscus paniscus</i>	♂	13	—	—	—	13	—	—	—	—	—	—	—	34	
<i>Ateles paniscus paniscus</i>	♀	14	—	—	—	1	13	—	—	—	—	—	—	34	
<i>Lagothrix lagotricha</i>	♂	12	—	—	—	—	—	—	—	—	—	3	9	62	
<i>Cebus albifrons</i>	♂	12	—	—	—	—	—	—	1	11	—	—	—	52	
<i>Cebus albifrons</i>	♀	7	—	—	—	—	—	—	—	7	—	—	—	52	
<i>Cebus</i> sp.	♂	13	—	—	—	—	—	—	—	—	—	13	—	54	
<i>Cebus</i> sp.	♀	12	—	—	—	—	—	—	—	—	1	11	—	54	

Table 2 presents the chromosome measurements in *Aotes trivirgatus*. The mean values were obtained from 4 mitotic plates.

The diploid chromosome complement of *Ateles paniscus paniscus* is composed of 34 chromosomes, with 2 metacentric, 13 submetacentric and 1 acrocentric pairs; the X chromosome is submetacentric and the Y is a small acrocentric [Plate 2(a, b)]. One submetacentric pair presents a deep secondary constriction (pair J). The only acrocentric pair present is the smallest of the complement. Chromosome measurements of *Ateles paniscus paniscus* were performed on 5 mitotic plates: 3 from female and 2 from male individuals (Table 3).

Lagothrix lagotricha exhibits 62 chromosomes with 2 metacentric, 13 submetacentric and 15 acrocentric pairs; the X chromosome is submetacentric and the Y a small acrocentric [Plate 1(d)]. Among the acrocentric pairs three show a deep secondary constriction. The first acrocentric pair stood out among the others because it is the longest.

Table 2

Chromosome length calculated as the mean percentages of the total haploid complement length (% TCL) of *Aotes trivirgatus*

Pair	% TCL	Pair	% TCL	Pair	% TCL	Pair	% TCL
A	7.44	H	4.10	L ₄	3.80	L ₁₁	2.44
B	5.37	I	3.69	L ₅	3.50	L ₁₂	2.48
C	5.05	J	3.68	L ₆	2.98	L ₁₃	2.41
D	4.98	K	3.30	L ₇	2.89	L ₁₄	2.07
E	4.50	L ₁	4.70	L ₈	2.88	X	5.90
F	4.18	L ₂	4.34	L ₉	2.67	Y	2.25
G	4.06	L ₃	3.87	L ₁₀	2.69		

Table 3

Chromosome length calculated as the mean percentage of the total haploid complement length (% TCL) of *Ateles paniscus paniscus*

Pair	% TCL	Pair	% TCL	Pair	% TCL	Pair	% TCL
A	11.30	F	6.65	K	4.74	P	2.07
B	9.76	G	6.01	L	4.32	X	5.80
C	7.79	H	5.63	M	4.13	Y	2.08
D	7.74	I	5.09	N	3.79		
E	7.71	J	5.04	O	2.64		

Table 4

Chromosome length calculated as the mean percentage of the total haploid complement length (% TCL) of *Lagothrix lagotricha*

Pair	% TCL	Pair	% TCL	Pair	% TCL	Pair	% TCL
A	6.18	I	3.32	P ₃	4.38	P ₁₀	2.08
B	4.81	J	3.10	P ₃	3.87	P ₁₁	1.99
C	4.35	K	3.13	P ₄	3.90	P ₁₂	1.62
D	4.31	L	2.82	P ₅	3.66	P ₁₃	1.52
E	4.00	M	2.44	P ₆	3.20	P ₁₄	1.56
F	4.08	N	2.24	P ₇	3.06	P ₁₅	1.52
G	3.63	O	2.00	P ₈	2.11	X	3.78
H	3.47	P ₁	5.78	P ₉	2.06	Y	0.86

The mean values of the chromosome measurements were obtained from 3 mitotic plates from the same specimen and the results are presented in Table 4.

The chromosome complement of *Cebus albifrons* is of 52 chromosomes with 1 metacentric, 8 submetacentric and 16 acrocentric pairs; the X chromosome is submetacentric and the Y a small acrocentric [Plate 3(a, b)]. The single metacentric pair is small. The first acrocentric pair appears to be dimorphic and the difference in length between the homologues is present in every male and female cell analysed. At least two acrocentric pairs revealed a deep secondary constriction in the long arms. Chromosome measurements of *Cebus albifrons* were performed on 4 mitotic plates: 1 from the male and 3 from the female specimen (Table 5).

The *Cebus* sp. individual exhibits 54 chromosomes with 1 metacentric, 10 submetacentric and 15 acrocentric pairs; the X and Y chromosomes are acrocentric [Plate 3(c, d)]. The single metacentric pair consists of small chromosomes. The first acrocentric pair is much longer than the other acrocentrics and it could consequently be clearly identified. At least two acrocentric pairs showed a deep secondary constriction in the long arms. Chromosomes were measured and the mean values of each chromosome pair were obtained from 4 mitotic plates: 1 from male and 3 from female individuals (Table 5).

Table 5

Chromosome length calculated as the mean percentage of the total haploid complement length (% TCL) of *Cebus albifrons* and *Cebus* sp.

<i>Cebus albifrons</i>				<i>Cebus</i> sp.			
Pair	% TCL	Pair	% TCL	Pair	% TCL	Pair	% TCL
A	6.39	J ₆	3.82	A	5.96	L ₄	4.04
B	6.19	J ₇	3.75	B	5.44	L ₅	3.93
C	5.75	J ₈	3.58	C	4.89	L ₆	3.91
D	4.59	J ₉	3.44	D	4.78	L ₇	3.58
E	4.42	J ₁₀	3.39	E	4.71	L ₈	3.31
F	4.13	J ₁₁	3.01	F	4.38	L ₉	3.00
G	3.96	J ₁₂	2.28	G	4.39	L ₁₀	2.78
H	3.55	J ₁₃	2.36	H	3.64	L ₁₁	2.44
I	2.32	J ₁₄	2.30	I	3.25	L ₁₂	2.49
J ₁	6.10	J ₁₅	1.64	J	2.47	L ₁₃	1.64
J ₂	4.79	J ₁₆	1.49	K	2.51	L ₁₄	1.65
J ₃	4.54	X	3.65	L ₁	6.22	L ₁₅	1.36
J ₄	4.29	Y	1.39	L ₂	4.92	X	3.98
J ₅	4.25			L ₃	4.33	Y	1.43

4. Discussion

Karyotype comparison between our *Alouatta fusca clamitans* and *A. caraya* studied by Egozcue & Egozcue (1966) reveals major differences in the diploid numbers and in the morphology of two chromosome pairs. *A. caraya* has 52 chromosomes while *A. fusca clamitans* has only 50 chromosomes. *A. caraya* has one pair of long acrocentric chromosomes (pair 2) which do not exist in the karyotype of *A. fusca clamitans*. This subspecies exhibits one pair of submetacentrics (pair A) which is absent in *A. caraya*. The length of the long acrocentric chromosome from the latter is quite similar to the long arm belonging to chromosome pair A of *A. fusca clamitans*. Centric fusion between a long acrocentric chromosome and a medium-sized acrocentric chromosome has presumably given rise to the submetacentric pair found in *A. fusca clamitans*.

Alouatta caraya has one pair of submetacentric chromosomes (probably pair 10) which is not observed in the complement of *A. fusca clamitans*. This species presents an acrocentric pair of similar size instead. Pericentric inversion might explain such a difference.

The above differences lead to the supposition that *Alouatta caraya* and *A. fusca clamitans* derived from a species with 52 chromosomes presenting 16 acrocentric pairs. Pericentric inversion in an acrocentric chromosome might have produced the karyotype found in *Alouatta caraya* with 15 acrocentric pairs and a centric fusion between two acrocentrics presumably originated the complement of *A. fusca clamitans* with 14 acrocentric pairs.

The complement of *Alouatta seniculus* is quite different from those of *A. caraya* and *A. fusca clamitans*. *A. seniculus* has 44 chromosomes with 2 metacentric, 6 submetacentric and 13 acrocentric pairs (Bender & Chu, 1963). Centric fusions and pericentric inversions would probably explain the origin of the karyotype of *Alouatta seniculus* as deriving from a karyotype with 52 chromosomes provided that intermediary karyotypes were also found. Staton (1967) suggested that centric fission might be the mechanism responsible for the differences between the chromosome complement of *Alouatta seniculus* and the karyotypes of the other *Alouatta* species described.

A diploid complement with 49 chromosomes was found in two males of *Alouatta fusca clamitans*. The paired chromosomes of these two males were compared with the karyotypes of male and female presenting 50 chromosomes. The unpaired chromosome of the male complement was a relatively large submetacentric. The missing chromosome might be the Y which could be attached to an autosome: it is in fact unlikely that the Y could be missed in apparently normal male mammals.

The single specimen belonging to *Alouatta villosa* (Hsu, 1965) reported in the literature had 53 chromosomes; therefore, its diploid number should be 54 or 52. Investigation of the karyotypes of all species and subspecies belonging to the genus *Alouatta* will indeed contribute to elucidate the evolutionary steps responsible for the emergence of this genus.

Comparison of the data presented above for *Aotes trivirgatus* with the complement with 54 chromosomes described by Egozcue *et al.* (1969) reveals few discrepancies. The specimen with 52 chromosomes [Plate 1(c)] had a large metacentric pair which is not present in *Aotes trivirgatus* with 54 chromosomes. This last specimen shows instead two identical large acrocentric pairs and a centric fusion between two acrocentric chromosomes could have produced the metacentric one. Brumback *et al.* (1971) described a similar fusion event in *Aotes trivirgatus griseimembra* ($2n = 54, 53$ or 52).

The results obtained for the species *A. trivirgatus* lead to the conclusion that it includes intraspecific variability which also occurs in *Cebus capucinus* in which a diploid complement with 52 or 54 chromosomes was described (Egozcue, 1969; Egozcue & Egozcue, 1966b).

Cebus albifrons had been reported with 54 chromosomes in its diploid complement (Egozcue & Egozcue, 1967). The male and female specimens dealt with in this paper had 52 chromosomes.

The individuals studied exhibited a largely dimorphic acrocentric pair in all cells. It could be the result of a segregating balanced translocation. Formerly, balanced translocations were described in Primate chromosomes by Egozcue *et al.* (1969). Moreover, Egozcue & Egozcue (1967) reported 5% of the cells of *Cebus albifrons* with a dimorphic acrocentric pair.

Comparisons between the karyotypes of *Cebus albifrons* also indicated that the specimens with 54 chromosomes had a submetacentric pair which was not observed in the individuals with 52 chromosomes. In *Cebus albifrons* with $2n = 52$, pair F is submetacentric and the corresponding one (pair 11) in *Cebus albifrons* with $2n = 54$ is described as metacentric. This morphologic difference could be interpreted as the result of a process of pericentric inversion. The submetacentric pair, not observed in the complement with 52 chromosomes, is difficult to explain, unless intermediary karyotypes are reported. Duplication of a chromosome pair would be a reasonable hypothesis to explain such a variation. Both diploid complements with 52 or 54 chromosomes displayed only one small metacentric pair.

A comparison between the diploid complement of *Cebus* sp. and *Cebus albifrons*, both with 54 chromosomes, revealed that the former had 15 and the latter 16 acrocentric pairs. A pericentric inversion process might explain the origin of the submetacentric pair F of *Cebus* sp. without correspondence in *C. albifrons*. The same process could also be attributed to the morphologic variation of the X chromosome.

Karyological investigations of different diploid complements of the species belonging to the genus *Cebus* have brought to light that intraspecific and interspecific variabilities and more frequent than previously suspected. Further analysis of species and subspecies composing the genus *Cebus* is relevant to establish the evolutionary steps within this genus.

The karyotype of *Ateles paniscus paniscus* does not basically differ, from the karyotypes already described for other species and subspecies of this genus. *A. paniscus paniscus* and *A. paniscus chamek* (Bender & Mettler, 1958) seem to have identical karyotypes: only the X chromosome is submetacentric in *A. paniscus paniscus* and metacentric in *A. paniscus chamek* (in both the Y chromosome is acrocentric).

The diploid complement of *Ateles geoffroyi* (Hsu & Benirschke, 1968; Egozcue *et al.*, 1969) shows minimal differences when compared to that of *A. paniscus paniscus*. Pair G of *A. paniscus paniscus* is submetacentric and the corresponding one in *A. geoffroyi* is metacentric. Both X and Y chromosomes of *A. geoffroyi* exhibit metacentric morphology (Hsu & Benirschke, 1968) but the X chromosome has also been described as submetacentric and the Y as metacentric (Egozcue *et al.*, 1969).

The diploid complement of *A. paniscus paniscus* is quite similar to that of *A. geoffroyi cucullatus* described by Bender & Mettler (1958). The discrepancy observed in the present investigation was that the X chromosome is submetacentric in the former but metacentric in the latter species. Furthermore, studies on *A. geoffroyi cucullatus* reported by

Egozcue & Hagemenas (1967) indicated that the X chromosome is submetacentric and the Y is either acrocentric or submetacentric.

Thus, intraspecific and interspecific variability in the genus *Ateles* seems to be greater for the sex chromosomes than for the autosomes. The karyotypic differences observed in several species of the genus *Ateles* probably are due to a pericentric inversion process.

Though both *Lagothrix* and *Ateles* belong to the subfamily *Atelinae*, the diploid numbers of chromosomes are very different. *L. lagotricha* has 62 chromosomes with 2 metacentric, 13 submetacentric, and 15 acrocentric pairs; the X chromosome is submetacentric and the Y is acrocentric. *L. lagotricha* was also reported by Egozcue & Perkins (1970) and the complement of the single female described by them showed 62 chromosomes with 16 submetacentric and 15 acrocentric pairs, but no information about the sex chromosomes was provided. This karyotype and the male chromosome complement reported in the present paper are very similar. It is therefore possible to suggest that the female third chromosome pair corresponds to the X pair.

The differences between *Ateles* and *Lagothrix* karyotypes are very difficult to explain through centric fission and or pericentric inversion. Staton (1967) believed that centric fission followed by pericentric inversions could be responsible for these discrepancies.

The morphology of the X chromosome varies in different species of Cebidae. The X chromosomes of *Alouatta seniculus* (Bender & Chu, 1963), *Cebus capucinus* (Egozcue & Egozcue, 1966b) and *Cebus apella* (Bender & Mettler, 1958) are acrocentric. Most species have a submetacentric X chromosome but intraspecific variability concerning its morphology is frequent. In *Cebus capucinus* the X chromosome has also been described as submetacentric (Egozcue, 1969); in *Aotes trivirgatus* the X chromosome was reported as submetacentric, but in the present investigation [and in that of Brumback *et al.* (1971)] this chromosome was seen to be metacentric.

In relation to the Y chromosome, some morphologic variations have also been found: the Y chromosome in the Cebidae is acrocentric in almost all species, but it is submetacentric in *A. seniculus*, acrocentric or metacentric in *Callicebus moloch* (Egozcue, 1969), acrocentric or submetacentric in *Ateles geoffroyi cucullatus* (Egozcue & Hagemenas, 1967; Bender & Mettler, 1958), and acrocentric or metacentric in *Aotes trivirgatus*.

The Y chromosome often corresponds to the smallest acrocentrics of the complement. In *L. lagotricha* the Y is still smaller with a relative value of 0.86% of the total X-containing haploid complement length. Therefore it is reasonable to suggest that there is a high degree of specialization in the Y chromosome underlying the processes of sexual differentiation.

In *A. fusca clamitans* an apparent absence of the Y chromosome was found in some specimens. Hsu & Hampton (1970) reported three types of sex determination systems in *Callimico goeldii* (family Callithricidae): the normal XX-XY system, the fusion of a small portion of the Y to an autosome and the fusion of the whole Y to an autosome.

The observations described herein suggest that some species of the Cebidae might also present an intraspecific polymorphism related to sex determination by the Y chromosome.

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M. A. Pereira da
Silva

*Instituto de Biofísica da
Universidade Federal do Rio de
Janeiro, Brazil and Laboratoire
d'Anthropologie Biologique,
University of Paris, France*

N. Petit-Maire

*Laboratoire de Géologie du
Quaternaire du CNRS, Meudon-
Bellevue, 9210 France*

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Symmetry and Asymmetry in Fingerprints of Three Genera of South American Monkeys in Relation to Morphological Evolutionary Problems

Fingerprints of South American monkeys of the genera *Alouatta*, *Ateles* and *Cebus* were studied. Dermatoglyphics were analysed in relation to pattern intensities; the distribution of symmetric and asymmetric designs was also determined. Results have been related to some aspects of the contribution of dermatoglyphics to the study of Primate morphological evolution.

1. Introduction

The dermatoglyphics of Primates have been widely studied by Whipple, Midlo, Biegert, Iwamoto, Brehme and others. The authors chiefly tried to compare the patterns found in different species in connection with different steps in the phylogenetic sequence. Whipple (1904) and Midlo & Cummins (1942) found a correlation between the distribution of some patterns considered as "primitive" with the degree of development of the animal deduced from other anatomical and physiological criteria.

Pereira da Silva, Petit-Maire & Rakotosamimanana (1972) found also a different degree of pattern types within the dermatoglyphic morphological plan in studying a small group of *Cebidae* (genera *Alouatta*, *Ateles* and *Cebus*).

Whorls, loops, arches, vestiges, open fields and composite figures are frequent patterns in the palms and soles of Primates and Man; in prosimians and lower Primates, whorls are practically the only patterns seen.

But according to the authors that studied Primate dermatoglyphics, whorls in monkeys have certain specific anatomical details that allow immediate differentiation from the whorls present in Man.

Also according to Midlo & Cummins (1942), a particular aspect of dermatoglyphics in Primates is the presence of whorls on the interdigital pads of the palms which is exceptional in the corresponding regions of the human palms (Pereira da Silva & Petit-Maire, to be published). In higher Primates, these patterns can also be found, though occurring less frequently.

Midlo & Cummins (1942) studied a great number of Primate dermatoglyphics from the most primitive to the upper species, including Man. They did not establish any specificity of patterns distribution as in Man but they confirmed the observations of Whipple for the higher frequency of whorls in the primitive species. Even this point is not considered absolute by Midlo, since whorls can also be a dominant pattern in some higher Primates and, as we know, even some human populations like the Eskimos (Ducros & Ducros, 1972) and the Alakaluf South American Indians (Pereira da Silva, to be published) present a high frequency of whorls in their fingerprints.

Considering the whole Primate order, the essential correlation that can be drawn between dermatoglyphics and other anatomical characters defining a phylogenetic sequence is expressed by the relative frequency of whorls.

In the present work we try to analyse previous results in order to study and to question the morphological development established by the usual anatomical and physiological criteria, in correlation to dermatoglyphic patterns. In the same way, we try to draw a comparison between the pattern distribution of dermatoglyphics according to more definite criteria of the use of the hand in Primates (Bishop, 1964).

2. Material and Methods

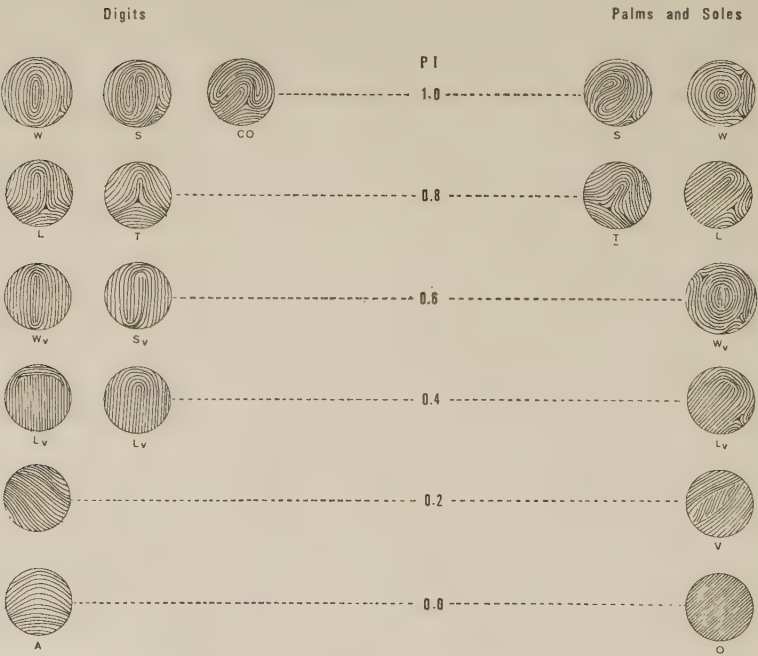
The Primates that have been studied in the present work belong to three genera of the *Cebidae* family from South American monkeys.

The 19 individuals belonged to the following species:

<i>Alouatta seniculus</i>	11 individuals: 6 males and 5 females
<i>Ateles belzebuth</i>	2 individuals: 2 females
<i>Cebus griseus</i>	6 individuals: 6 females

The dermatoglyphics were taken by Petit-Maire from animals captured in Venezuela.

Figure 1. Most common patterns on digits, palms and soles of the Primates and corresponding pattern intensity. W = Whorl; S = double whorl or S pattern; Co = composite pattern; L = loop; T = tented arch; Wv = vestigial whorl; Sv = vestigial double whorl; Lv = vestigial loop; V = vestiges; A = arch; O = open field; P.I. = pattern intensity.



The method utilized for analysing dermatoglyphics is that described by Midlo & Cummins (1942). The quantitative value, as for Man, was adopted to represent one character or different ridge configurations.

This quantitative value is defined as pattern intensity (P.I.) and it establishes a definite value for the variability of configurations (Figure 1).

Configurations as whorls or similar double whorls, S patterns are 1.0 P.I.

Configurations as loops and tented arches are defined as 0.8 P.I.

Configurations as degenerate and vestigial whorls are defined as 0.6 P.I.

Configurations as degenerate and vestigial loops are defined as 0.4 P.I.

Configurations as vestiges are defined as 0.2 P.I.

Configurations as open fields are defined as 0.0 P.I.

Using these values defined by Midlo & Cummins, we established the total pattern intensity (T.P.I.) for the pads of the palms and soles.

3. Results and Discussion

Figure 2 gives results about P.I. distribution.

Our data are very similar to that of Midlo & Cummins (1942) for *Alouatta*, *Ateles* and *Cebus*. The P.I. on palms are higher than those on soles. *Cebus* has palm and sole differences more important than *Alouatta*. In Midlo and Cummins's samples, as in those of other authors, the values of the P.I. on palms are usually greater than those on soles, *Cercocebus* genera excepted.

When our data on the regional distribution of P.I. are compared with those obtained by Biegert (1971) and Brehme (1967, 1968) we can see that *Alouatta*, *Ateles* and *Cebus* genera usually have a more important P.I. distribution in the interdigitals and hypothenar regions as the Primates studied by these authors (Figures 3 and 4). In other words, the

Figure 2. Distribution of pattern intensity on palms and soles in a series of Primates including our data (modified from Midlo & Cummins, 1942). ▲, Our data for palms; △, our data for soles.

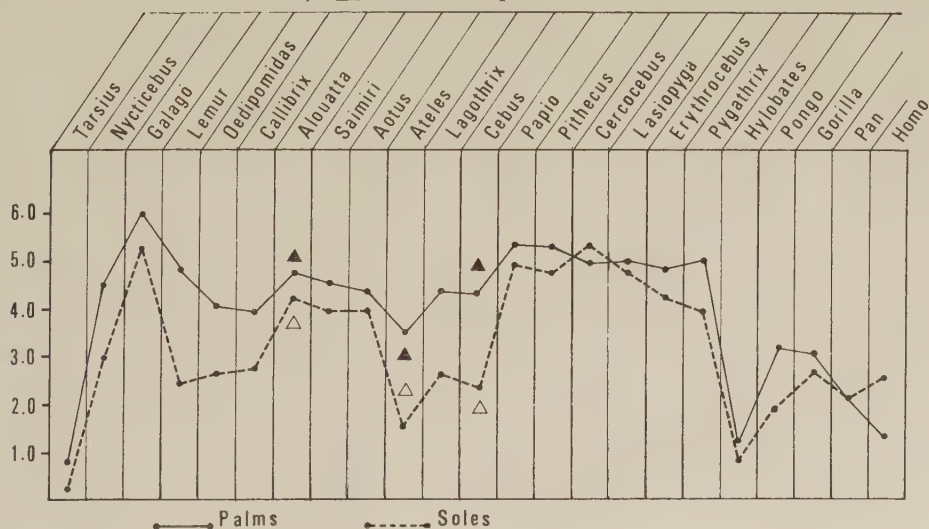
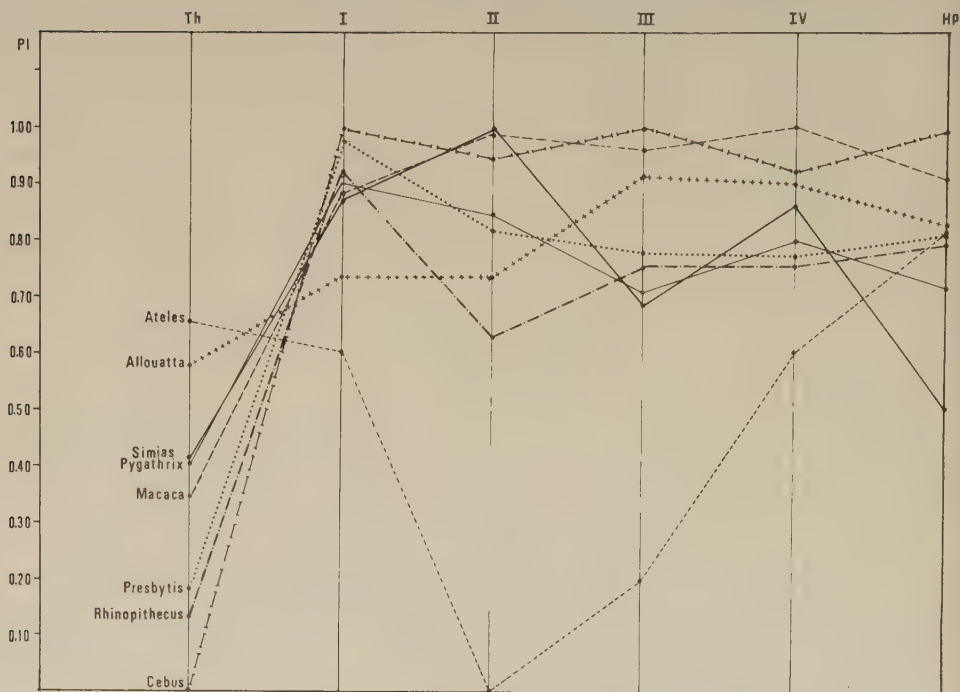


Figure 3. Regional pattern intensity distribution on the palms in a series of lower Primates including Brehme and our data (modified from Biegert, 1971). P.I. = Pattern intensity; Th = thenar region; Hp = hypothenar proximal region; I = first interdigital region or first interdigital pad; II = second interdigital region or second interdigital pad; III = third interdigital region or third interdigital pad; IV = fourth interdigital region or fourth interdigital pad.



P.I. of the hypothenar region of the palm is higher than the P.I. of the thenar region. Consequently, as concerns the ulnar and radial sides of the P.I. on the palms, in our series as in all Primates the same tendency is shown, namely higher P.I. on the ulnar side. However, lower Primates as *Alouatta*, *Ateles* and *Cebus* present for both sides higher values of P.I. than more developed Primates.

A different situation is observed for the P.I. on the soles: in lower Primates, in which our series is included, no general tendency of distribution on the ulnar and radial side (or hypothenar and thenar regions) appears. More developed Primates however present a general tendency towards higher values of P.I. on the radial side, but not so clearly defined as on the palms (Figures 5 and 6).

As regards palm and sole patterns, lower and higher Primates also show a different situation compared to Man. While, in Man, an asymmetrical distribution of P.I. values is observed with higher values for the sole, Primates behave as follows (Figure 7): higher Primates show an opposite asymmetry with high values for the P.I. on palms; lower Primates in which our series is included do not show a unique tendency with respect to anterior and posterior limbs. Some groups present symmetric values, others asymmetric values, either with high values for soles or for palms. In any case, however, lower Primates present P.I. values pronouncedly higher than those of Man or more advanced Primates.

Figure 4. Regional pattern intensity distribution on the palms in a series of Hylobatidae and Pongidae (modified from Biegert, 1971). P.I. = Pattern intensity; Th = thenar region; Hp = hypothenar proximal region; I = first interdigital pad; II = second interdigital pad; III = third interdigital pad; IV = fourth interdigital pad.

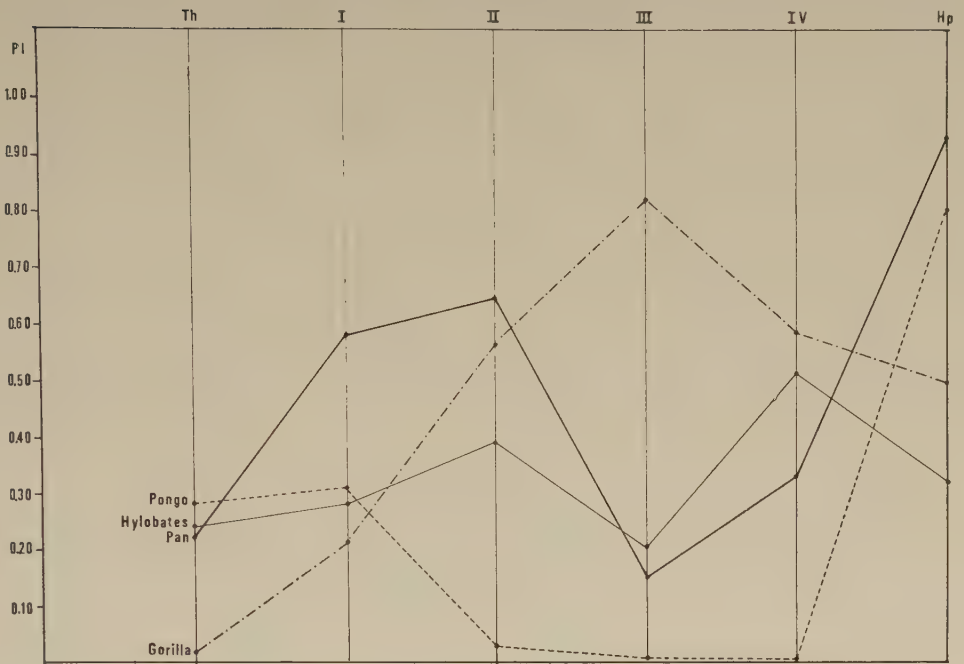


Figure 5. Regional pattern intensity distribution on the sole in a series of lower Primates including Brehme and our data (modified from Biegert, 1971). P.I. = Pattern intensity; Thp = thenar proximal region; Hd = hypothenar distal region; I = first interdigital pad; II = second interdigital pad; III = third interdigital pad; IV = fourth interdigital pad.

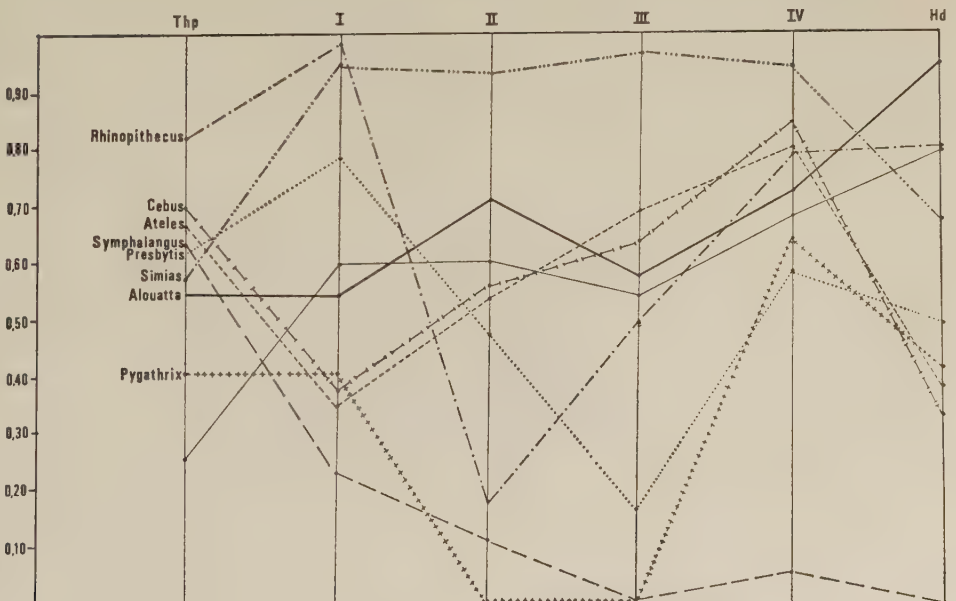


Figure 6. Regional pattern intensity distribution on the sole in a series of Pongidae (modified from Biegert, 1971). P.I. = Pattern intensity; Thp = thenar proximal region; Hd = hypothenar distal region; I = first interdigital pad; II = second interdigital pad; III = third interdigital pad; IV = fourth interdigital pad.

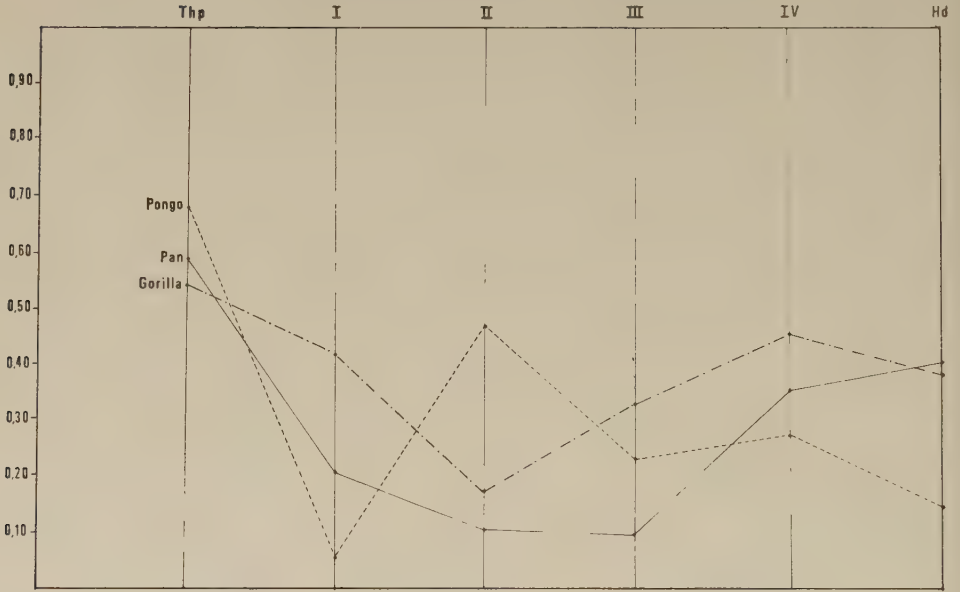
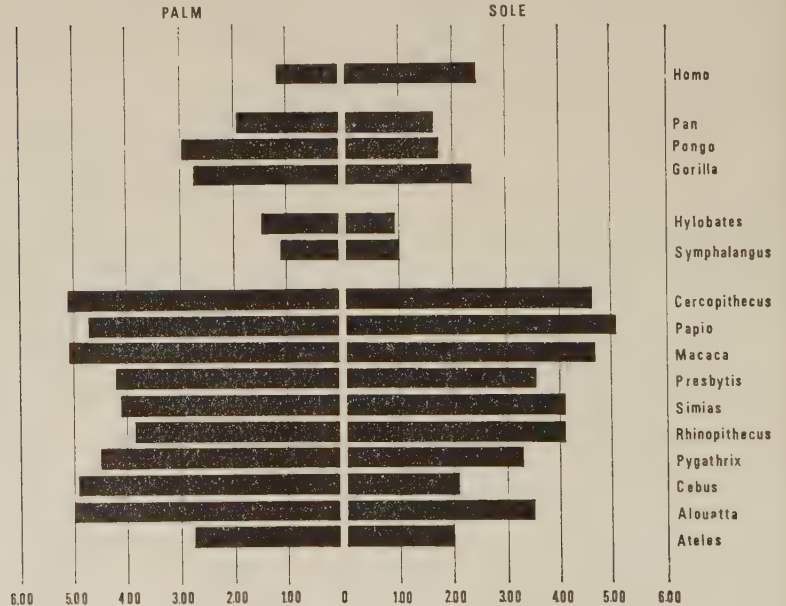


Figure 7. Distribution of P.I. on palms and soles in a series of Primates including Man in regard to the symmetry and asymmetry of values (modified from Biegert, 1971 with Brehme and our data).



4. Conclusions

The general conclusions to be drawn from the P.I. analysis of palms and soles in our series compared to other Primates, as regards the regional distribution of patterns on the palms and soles, taking also the functional differences between the anterior and posterior limbs into account, are the following:

- (1) Higher Primates show a pronounced concentration of patterns on the ulnar side of the palms or hypothenar regions and on the tibial side or the thenar regions of the soles;
- (2) Lower Primates, in which our series is included, show the same tendency for the palms but a variable pattern concentration for the soles;
- (3) In both higher and lower Primates, a pronounced difference exists in the distribution of patterns between palms and soles, which probably reflects the functional differentiation of anterior and posterior limbs;
- (4) As concerns the distribution of patterns on palms and soles, different steps can be recognized for Man, for the higher and for lower Primates.

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P. Perticone
M. Rizzoni
F. Palitti
P. di Chiara

Banding Patterns of the Chromosomes of the Rhesus Monkey (*Macaca mulatta*)

The Rhesus monkey (*Macaca mulatta*) has 21 pairs of chromosomes, many of which can easily be confused with one another by the traditional staining methods. By using the method of banding with trypsin (Seabright, 1971) we have been able to characterize the various pairs of homologous chromosomes and we have classified them by following the criteria adopted by Rothfels & Siminovich (1958). The evolutionary meaning of the results are discussed.

*Centro di Genetica Evoluzionistica
del C.N.R. e Istituto di Genetica,
Città Universitaria,
Roma, Italy*

Received 18 August 1973 and
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1. Introduction

The 21 pairs of chromosomes of the Rhesus monkey (*Macaca mulatta*) have been classified according to various criteria: Rothfels & Siminovich (1958) classified them into three natural groups, on the basis of their dimensions: long (Nos. 1–7), medium (8–17) and small (18–21); the *X* chromosome is a medium metacentric, the *Y* a very small telocentric. Another classification, given by Chiarelli (1962a) and based on the arm ratios, divides them into three groups: sub-telocentrics (1–13), metacentrics (14–19) and atypical (sex and marker chromosomes).

Classical staining techniques enable one to pursue the analysis within these groups only in certain cases and with considerable difficulty. The only chromosomes that can be definitely recognized are the large metacentric (chromosome no. 5, according to Rothfels & Sininovich) and a medium metacentric characterized by an extensive secondary constriction at the centromere (no. 9).

From this point of view the new chromosome banding techniques have made it far easier to identify the various pairs of homologous chromosomes in those species in which many chromosomes are very similar to one another: Man (Caspersson *et al.*, 1970), the mouse (Francke & Nesbitt, 1971), etc.

In this work we have tried to characterise and identify the chromosomes of the Rhesus monkey (*Macaca mulatta*) by means of the trypsin-banding technique.

2. Materials and Methods

Primary cultures were prepared from the kidneys of four male Rhesus monkeys by breaking down the cells of the organ with trypsin (Moscona, 1952); the specimens were supplied by the Istituto Superiore di Sanità in Rome.

The cells were grown in Earle's minimum essential medium (MEM), with the addition of 2% glutamine and 15% fetal calf serum. The cultures were fixed 4 and 8 days after planting. The cells were treated with 10^{-7} M-colchicine 12 hr before fixation. After a 20 min hypotonic treatment with 0.03 M-KCl, the cells were fixed with 3:1 methyl alcohol:acetic acid, according to the air-drying technique (Moorhead *et al.*, 1960). Trypsin banding was carried out by following, with slight modifications, the method

described by Seabright (1971). About 40 fully spread metaphase plates (10 for each specimen) were photographed and karyotyped.

Chromosome measurements were carried out on 12 cells (3 for each specimen). For each chromosome, the percentage of the total length of the haploid genome (non-autosomal, including the X chromosome) (TCL) and the ratio between the arms (AR = long/short) were calculated. For the classification and measurement of the chromosomes the method followed was that of Rothfels & Siminovich (1958).

3. Results

The trypsin banding technique provides an extremely specific and constant pattern by which each pair of homologous chromosomes can easily be identified as is shown in Plate 1. Results of the calculations of TCL and AR are summarized in Table 1. In all the metaphases studied, we encountered no polymorphisms of the banding patterns.

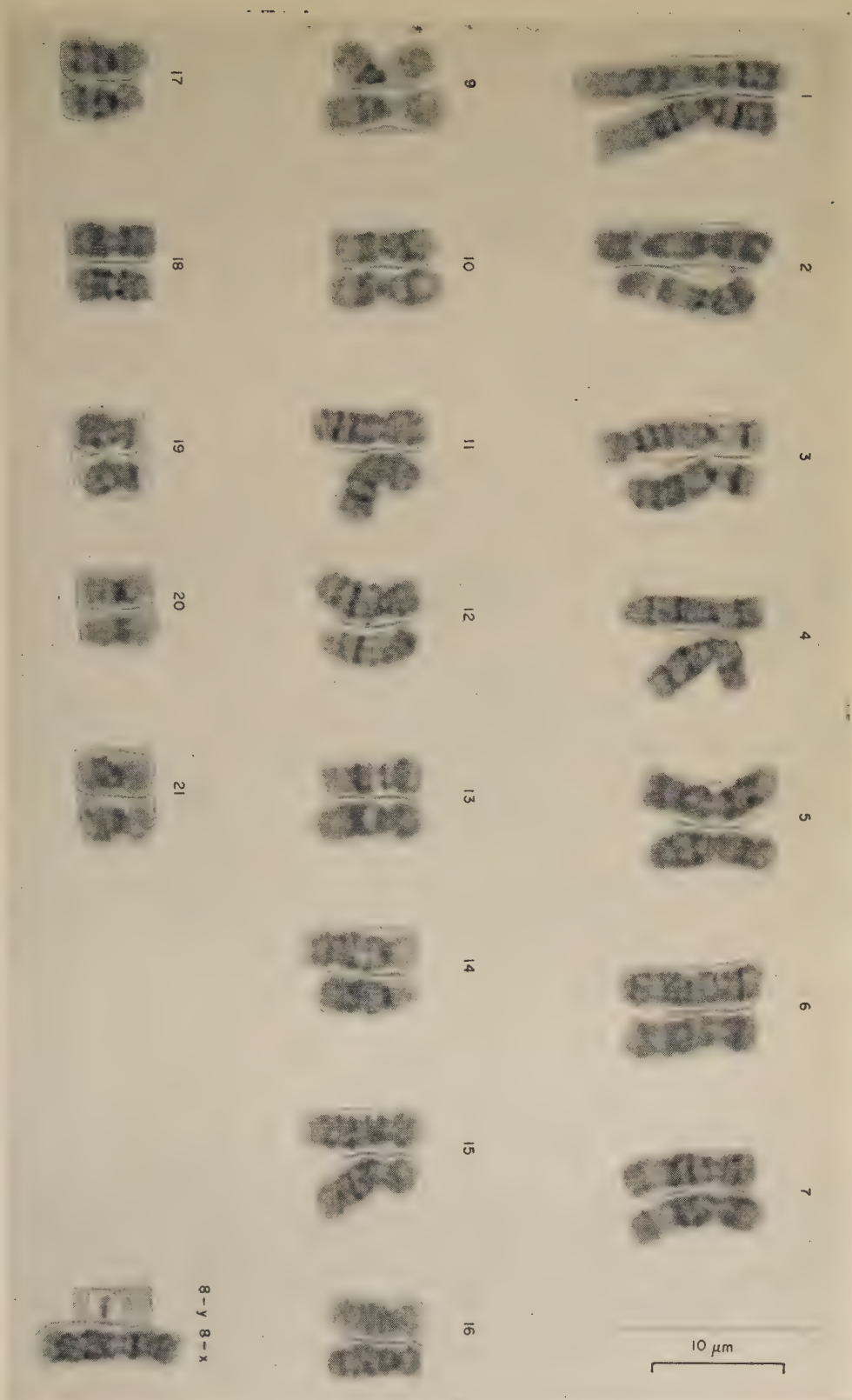
Table 1 % Haploid "total chromosome length" (TCL) and arm ratios of the chromosomes in male *Macaca mulatta*

Chromosome no.	% Haploid TCL		Arm ratio	
	Mean	S.E.	Mean	S.E.
1	7.70	0.22	1.56	0.07
2	6.26	0.12	1.90	0.06
3	6.10	0.13	2.07	0.08
4	5.86	0.13	1.95	0.09
5	6.00	0.11	1.29	0.03
6	5.91	0.10	2.48	0.10
7	5.77	0.12	2.48	0.15
9	4.76	0.13	1.27	0.03
10	4.52	0.12	1.30	0.10
11	4.75	0.08	1.82	0.09
12	4.50	0.14	2.05	0.10
13	4.49	0.10	2.32	0.15
14	4.13	0.08	2.36	0.10
15	4.49	0.09	2.37	0.10
16	3.94	0.08	2.57	0.14
17	3.30	0.07	1.85	0.08
18	3.56	0.11	1.17	0.20
19	2.96	0.07	1.54	0.08
20	2.85	0.09	1.22	0.06
21	2.85	0.06	1.36	0.06
x	4.62	0.16	1.12	0.22
8				
y	1.03	0.07	—	—

The characteristic pattern of each pair of homologous chromosomes is described as follows:

- No. 1: TCL = 7.70; AR = 1.56. Short arm: 4 bands, clearly distinct from each other. Long arm: 1 band just below the centromere, 4 other bands, of varying size, are set close together midway down the long arm, ending in a long interband.
- No. 2: TCL = 6.26; AR = 1.90. Short arm: 2 large bands, one just above the centromere, the other in the distal part. Long arm: 2 bands just below the centromere, and a third band in the distal part.
- No. 3: TCL = 6.10; AR = 2.07. Short arm: 1 band in a subterminal position. The centromere is banded. Long arm: 6 clearly distinct and regularly spaced bands.

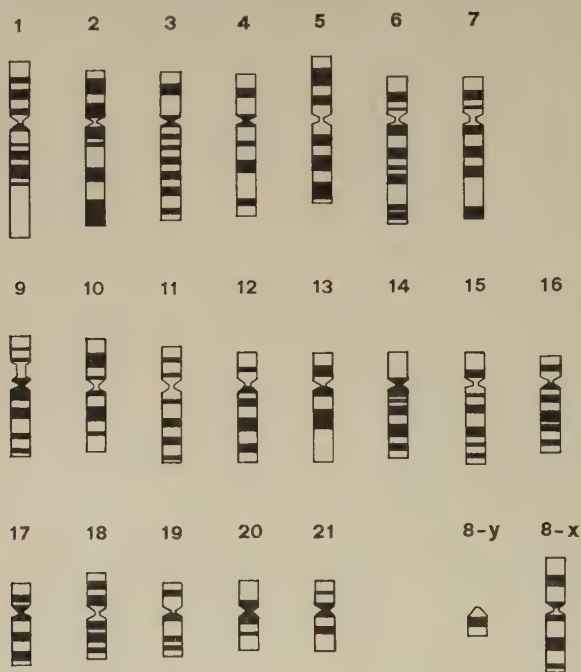
Plate 1. Caryogram of a C-metaphase of a diploid cell of a male *Macaca mulatta*.





- No. 4: $TCL = 5.86$; $AR = 1.95$. Short arm: 1 band in the middle. The centromere is banded. Long arm: 3 widely spaced bands, the middle one being the largest, and a large interband in the distal position.
- No. 5: $TCL = 5.86$; $AR = 1.95$. Short arm: 2 regularly spaced bands. Long arm: 3 regularly spaced bands.
- No. 6: $TCL = 5.91$; $AR = 2.48$. Short arm: 2 bands, one large one in the middle of the arm and a fine band proximal to the centromere. Long arm: 1 band just below the centromere, 3 bands midway down, and 2 bands at the distal extremity.
- No. 7: $TCL = 5.77$; $AR = 2.48$. Short arm: 2 bands. Long arm: 4 bands, one in a proximal position to the centromere, 2 midway down the arm, and one in a distal position.
- No. 8: See sex chromosomes.
- No. 9: $TCL = 4.76$; $AR = 1.27$. Short arm: a large non-banded secondary constriction on the distal side of which are 2 small bands. The centromere is banded. Long arm: the portion proximal to the centromere is banded; 3 other evenly spaced bands are visible.
- No. 10: $TCL = 4.52$; $AR = 1.30$. Short arm: 1 broad band midway down, 1 small band proximal to the centromere. Long arm: 1 small band near the centromere, 1 large band midway down and 1 small band in a distal position.
- No. 11: $TCL = 4.75$; $AR = 1.82$. Short arm: 2 bands. Long arm: 4 bands. All 6 bands are regularly spaced.
- No. 12: $TCL = 4.50$; $AR = 2.05$. Short arm: 1 band in the middle. Long arm: 1 band near the centromere and 3 others along the arm, the middle one being the largest.
- No. 13: $TCL = 4.49$; $AR = 2.32$. Short arm: 1 large central band. Long arm: 2 large bands, one just below the centromere and one midway down.
- No. 14: $TCL = 4.13$; $AR = 2.36$. Short arm: 1 band proximal to the centromere. The centromere is banded. Long arm: 5 bands, one proximal to the centromere. Of the other 4, the two middle ones are the largest.
- No. 15: $TCL = 4.49$; $AR = 2.37$. Short arm: 1 band proximal to the centromere. Long arm: 5 bands of equal size, with a broad interband between the 2nd and 3rd bands.
- No. 16: $TCL = 3.94$; $AR = 2.57$. Short arm: 1 band in the middle. Long arm: 5 regularly spaced bands, one being just below the centromere; the 2nd and 3rd bands from the centromere are the thickest.
- No. 17: $TCL = 3.30$; $AR = 1.85$. Short arm: 2 bands, one proximal to the centromere. Long arm: 3 bands, one proximal to the centromere and the other two regularly spaced.
- No. 18: $TCL = 3.56$; $AR = 1.17$. Short arm: 2 bands. Long arm: 3 bands.
- No. 19: $TCL = 2.96$; $AR = 1.54$. Short arm: 1 band. Long arm: 3 bands, one of which is just below the centromere. The other 2 are in a distal position.
- No. 20: $TCL = 2.85$; $AR = 1.22$. Short arm: no bands. The centromere is clearly banded. Long arm: 1 thin band.
- No. 21: $TCL = 28.5$; $AR = 1.36$. Short arm: 2 bands, one proximal to the centromere. The centromere is banded. Long arm: 2 bands, one proximal to the centromere.
- No. 8-X: $TCL = 4.62$; $AR = 1.12$. Short arm: 2 bands, one just above the centromere and the other midway down the arm. Long arm: 3 bands, one just below the centromere, a broader one in the middle and a thin one in a distal position.

Figure. 1. Scheme of the banding patterns: (T-G) bands of the 21 chromosomes of the *Macaca mulatta* complement.



No. 8-Y: TCL = 1.03. 1 band below the centromere.

The characteristics described above are shown diagrammatically in the idiogram in Figure 1.

4. Discussion

The banding patterns of the Rhesus chromosomes have been characterized so that they could be identified unequivocally. The importance of this animal for various clinical studies and the considerable interest surrounding evolutionary genetic studies comparing the genomes of the Primates both with one another and with those of man (Darlington & Hague, 1955; Chu & Bender, 1961; Chiarelli, 1962*a,b,c*, 1966*a*) should make this data of interest in many fields. A considerable impetus has recently been given to these studies by banding techniques, which make possible more thorough comparisons between individual chromosomes. (Chiarelli, 1972; Egozcue, 1973).

The choice of the Seabright method was dictated by the speed and facility of the technique and by the high resolution obtained. The characterization of the banding pattern is extremely specific since nearly all the chromosomes show characteristic bands that allow easy identification. The only difficulties that may arise in classification concern chromosomes nos. 6 and 7, whose short arms are identical and can be differentiated only by the presence of 2 small extra bands on the long arm of no. 6 (the 3rd and 5th from the centromere), which may not be easily distinguishable. Less difficulty is encountered in distinguishing chromosome 11 from 12, 15 from 16, and 10 from 8-X. In these cases, though a similarity exists in the banding pattern, there are discriminating elements that enable individual chromosomes within these pairs to be distinguished. In the first case,

the AR of chromosome 11 is lower than that of 12 (i.e. the short arm is larger and shows one band more than 12); in the 2nd case, the chromosomes can be discriminated by their size; 15 has a far greater TCL than 16; and in the 3rd case, pair 10 shows a greater AR.

Some chromosomes of the Rhesus are very interesting for the cytotaxonomy of the primates. For example, chromosome no. 6 and no. 13 seem to be present with a constant pattern in all the catarrhine (Egozcue, 1973). But perhaps the most interesting one is chromosome no. 9, marked by a long, achromatic secondary constriction, and a linear satellite.

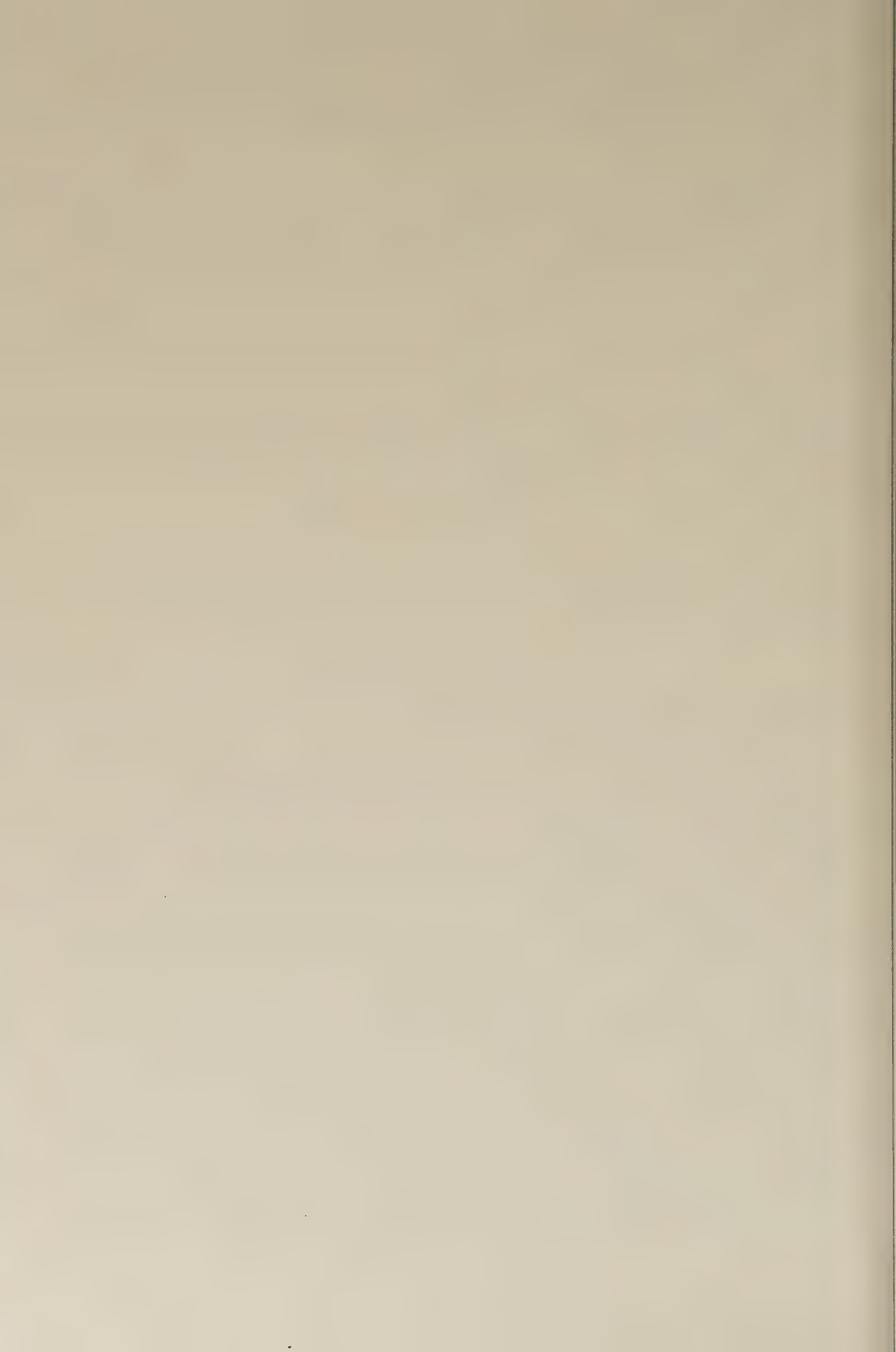
This chromosome is present in all catarrhine monkeys, except Man, anthropoids apes, and *Symphalangus syndactylus* (Chiarelli, 1966b). It is metacentric in the genera *Macaca*, *Papio*, *Cercocebus*, *Theropithecus*; the unmarked arm becomes shorter in the genera *Colobus*, *Presbytis* and *Hylobates*, and is almost lacking in the genus *Cercopithecus*. These differences appear to be due to translocations or deletions. For these properties, chromosome no. 9 could be a marker of the evolution of the old world Primates (Chiarelli, 1966b).

We think that the clear banding pattern of this chromosome allows a more detailed analysis which can lead to the identification of the single event of its transformation and solve some problems of the phylogenesis of the order Primates.

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Sheryl Green
Stanton Green
Georges J. Armelagos

Settlement and Mortality of the Christian Site (1050 A.D.–1300 A.D.) of Meinarti (Sudan)

*Department of Anthropology,
University of Massachusetts,
Amherst, Massachusetts, U.S.A.*

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Demographic analysis of cemetery data can be a useful complement to archaeological studies. Skeletal remains, when they comprise a representative sample, can serve to define certain relationships between the cultural and biological aspects of human adaptation. Furthermore, differential mortuary practices often mirror the status system of a society.

Specifically, this paper examines the status system and mortality pattern of the community of Meinarti in the Sudan. Stationary life table analysis shows age, sex, and an additional factor (reflected in survival) as determinants of status. In addition, the analysis of mortality supports Adam's hypothesis of village growth and decline.

1. Introduction

The reconstruction of a prehistoric social system often necessitates extensive analysis of fragmentary materials. In order to overcome this shortcoming, archaeologists have utilized methods derived from such disciplines as: geology (Vita Finzi, 1963), botany (Helbaek, 1963), demography (Birdsell, 1957), ecology (Hole, Flannery & Neely, 1969), and geography (Longacre & Reid, 1972), to aid and supplement their analysis. In addition, a variety of approaches have been utilized to increase the quantity and quality of information extracted from the excavation. One such approach, settlement archaeology, employs the concept of community in its analysis of the artifact in time and space. This concept can be complemented and enhanced by the population analysis of the physical anthropologist. At sites where sufficient skeletal remains exist, paleodemographic analysis integrates information concerning the settlement patterns with population structure, thus providing additional insights into the social system of the group.

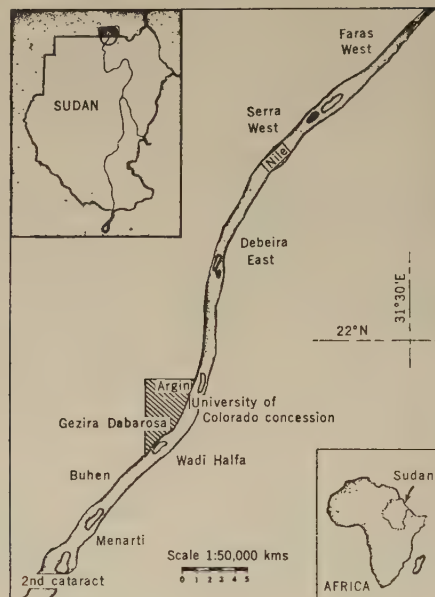
The settlement approach arranges the data so as to reflect the behavior of the social group. Research, therefore, not only stresses the information obtained about the artifact, but also emphasizes the spatial and temporal dimensions which define the social activities that produced it. The boundaries delimiting these social activities have been defined as the community (Chang, 1965:3). The archaeologist, lacking any observable activity, must rely on the remains of these activities, i.e. the archaeological settlement, in delimiting the community. The settlement approach, by focusing on the material remains, thereby defines the limits of the prehistoric population.

To further the scope of the community approach, skeletal remains, when they comprise a representative sample, can serve to define various relationships between the cultural and biological aspects of human adaptation. The cemetery provides information used in both estimating the vital statistics of the population and in defining its parameters. Data from a Christian site (1050 A.D.–1300 A.D.) on the island of Meinarti in Sudanese Nubia (Figure 1) will be used to discuss the relationship of the settlement pattern to the demographic structure of the group.

2. The Analysis of Mortality Data

The basis for paleodemographic analysis is the sex and age at death of skeletal remains. The data may be subjected to various methods of analysis. Two methods have had

Figure 1. Map of Nubia noting the location of the site of Meinarti.



widespread use. The first compares the percentages and proportions of age groups (infants, children) of the population under study (Angel, 1969). The second method, survival curve analysis (Blakely, 1971), depicts the cumulative percentage of survivors at the end of arbitrarily selected age intervals and thus visually presents the mortality trends of the population. The curve is charted by assuming an initial population of 100 % with each point subsequently derived by subtracting the percentage of deaths during the successive age intervals. One problem in utilizing survival curves stems from their cumulative nature since the first values directly affect the latter ones. If, for example, the initial values of two populations differ greatly, this difference will be reflected throughout the graph. Relative changes of mortality, reflected by the slope of the lines, therefore, remain the only means of graphic comparison.

In an effort to find a more effective method of analysis and comparison, anthropological demographers have recently revived the use of the life table (Swedlund & Armelagos, 1969; Acsadi & Nemeskeri, 1970). These tables consist of a series of population attributes calculated from the mortality data. In addition to survivorship, life expectancy (e_x) and the probability of dying at age x (q_x) can also be calculated in the life table. The latter two are not cumulative and are, therefore, useful in comparative analysis. The life table reflects the fluctuating nature of mortality with respect to age and highlights critical age intervals for mortality in a population (Swedlund & Armelagos, 1969). In other words, age specific differences in mortality enhance inter- and intrapopulation comparisons.

The specific type of life table proposed for paleodemographic analysis is the composite life table. Devised by field ecologists, it is based on the age of animals at death regardless of the exact year of their birth or death (see Deevey, 1947; Quick, 1963). Thus the composite life table treats a cross-sectional sample of the population (more than one cohort at a single point in time) as a representative sample of that population through time. The limitations of this method of sampling are that it assumes (1) a constant probability of dying with respect to age through time, and (2) the absence of migrations

during the time period under study. Although no human population is constant through time, prehistoric populations are generally assumed more stable than modern populations in terms of mortality because of their lack of rapid nutritional and medical improvements. Migrations must be investigated archeologically and, if possible, historically, for each specific case (Swedlund & Armelagos, 1969).

Once the applicability of the life table is established, a further methodological problem involves the cemetery as a random or representative sample of the population under study. Criticism concerning this assumption has centered on the representation of infants and children in cemetery populations. It has been argued that differential burial practices and differential preservation serve to underrepresent infants and children making it inapplicable for life table analysis.

Regarding the first point, the critics note that in many societies infants and children are not formally buried with adult members in a cemetery but are, rather, discarded more casually. Secondly, it has been argued that infant's and children's bones decompose more rapidly than adult's bones and are thus less likely to be found in cemeteries. While the first observation is substantiated by ethnographic fact, it should not be taken as given. Since the mortuary practices of a society are regulated by its religious ideology, knowledge of this ideology can be used to predict the burial practices for the different segments of the population.

Returning to the second point, we do not find it verified archaeologically. If conditions are sufficient for the preservation of adult burials, complete and careful excavation of infant burials should recover at least some remains (i.e. dentition). Underestimates of the number of children deriving from differential preservation can, therefore, be attributed to a failure to completely excavate a cemetery for fragmentary remains.

Even accepting these limitations, life table analysis can be used to resolve the problems of an underrepresentation of children. The non-cumulative nature of the life table functions e_x (life expectancy at age x), and q_x (the probability of dying at age x), permits the truncation of the possibly distorted infant mortality statistics and, therefore, allows the paleodemographer to make statements about the remaining segment of the population. In such a manner, mortality analysis of the adult portion of a population can be done without the influence of possibly biased infant statistics.

3. Nubian History

Nubia, a region located in the Middle Nile Valley, includes the area between the first to the fourth cataract. It extends from Egypt to the North into the Sudan in the South. Traditionally, interest has centered on Nubia's role as a corridor between the distinct cultural centers of sub-Saharan Africa and Egypt. Much research has, therefore, been concentrated on studying its historical, cultural and biological changes.

Ecologically, Nubia's history has been constantly affected by rainfall, the level of the Nile, and sand accumulation. Throughout the time period under study (1050 A.D.–1300 A.D.), the geologic studies of stratigraphic remains have suggested the absence of any major deluges of rain. This, however, did not eliminate the river's unpredictable annual fluctuations which produced its share of crop failures and flooding. During the Christian period (1050 A.D.–1300 A.D.) Meinarti was also overcome by one of the three advances and accumulations of sand which occurred during the island's history.

Historically, the mid-sixth century dates the conversion of Lower Nubia to Christianity

(Adams, 1967:7). Initially controlled by Egypt, the church later rose up to become the focus of Nubian independence (Adams, 1968). By classic Christian times (850 A.D.–1150 A.D.) Nubian influence had spread into upper Egypt, but by the late Christian period (1150 A.D.–1300 A.D.) the Nubian populations were confined to fortified centers. In addition, populations during the late Christian period were involved in increased warfare and continued harassment by nomads from the northern and southern Sahara, culminating in the disintegration of the Nubian church. Accumulation of sand and the flooding of the Nile contributed to the eventual abandonment of Lower Nubia during the fifteenth century.

The island of Meinarti is situated in the second cataract of the River Nile, while the site, which has remained stationary through its occupation, is located on the southern half of the one kilometer by one-half kilometer island. As an island, community activities were delimited by its physical boundaries. Basic activities were divided into farming, on the alluvium surrounding the village, and social and domestic activities within the village. Excavations have yielded 10 m of stratified deposits which reveal occupation, sand accumulation and flooding.

Excavation and analysis undertaken by W. Y. Adams (1964, 1965, 1967) show continuous occupation beginning around 200 A.D. and continuing until 1300 A.D. The strata have been divided into 18 occupation layers of which six represent large scale rebuilding and remodeling of the village. This paper will be limited to the macrostrata 9–7 (1050 A.D.–1150 A.D.) and 6–4 (1150 A.D.–1300 A.D.).

According to Adams (1968) at the beginning of the Christian period (levels 9–8: 1050 A.D.–1100 A.D.) the village appeared abandoned, then rebuilt within a few years. The patterns of settlement reminiscent of a previous state transmit a feeling of safety from the flood danger which plagued the preceding period. Spaciousness, a characteristic of the settlement, was conveyed through a large open plaza and large rooms. Communal activity is suggested by the planned construction of the village and its complexity. In addition, the church was restored to a plan which had originated in the preceding period. Levels 9–8 seem to indicate a time of cultural growth and security at Meinarti (Adams 1968).

Throughout the next level (level 7:1100 A.D.–1150 A.D.) sand was drifting and accumulating against the buildings. Village construction appeared to respond to this stress with buttresses, walls and blocked doors to combat the sand. Before final abandonment of the village the houses were bricked suggesting plans to return. Within a few years, sand had completely covered the village.

Meinarti was again reoccupied around 1150 A.D. (level 6). The village now contained two separate areas, the village proper and what has now been determined to be a granary (Adams, 1967). Built on top of the roofs of the previous level's houses, the new heavily walled separate unit structures represent an "expression of rebellion against previous times and perhaps a symptom of decay of the central polity" (Adams 1968:190). During this period, the village was again abandoned leaving material goods intact. Upon re-occupation, new houses with walls and brick vaulted roofs were again built on the old houses. A lookout tower was erected within the area of the granary. These trends in construction substantiate the historical evidence that Meinarti was frequently under the stress of enemy attack.

A cemetery located adjacent to the church was used continuously from A.D. 1050 until A.D. 1350 (levels 9–4). The cemetery was expanded vertically since accumulating sand

continually covered burials thereby providing new surfaces for interment. The periodic whitewashing of the church and its subsequent splatter along the ground provide the means to stratigraphically correlate the cemetery levels with those of the village. This relationship provided the key to linking the burial populations with their appropriate communities. Within the cemetery, burials are differentiated by the appearance of superstructures (mudbrick structures $2\text{ m} \times 1\text{ m} \times 60\text{ cm}$) which are found on top of a portion of the graves.

4. Analysis of Meinarti Mortality Data

The complete excavation of all levels of the Meinarti cemetery provides the essential mortality data for analysis. The data include the age and sex of each burial, its provenience (stratigraphic level) and the presence or absence of an accompanying superstructure.

The superstructures atop a portion of the burials of levels 9–7 form the focus of several problems. The first problem concerns the status system of the village of Meinarti as reflected by differential mortuary practices. In regard to this problem, the following hypotheses were tested:

- (1) Age was a factor determining an individual's status.
- (2) Sex was a factor determining an individual's status.
- (3) The mortality patterns of the groups with and without superstructure reflect biological differences in terms of survival and thus suggest a third status factor.

The assumption underlying these hypotheses is that differential mortuary practices mark the status of the buried individual. This assumption is supported by several observations. Firstly, the building of a superstructure requires time, labor and materials. The fact that not all burials are accompanied by superstructures indicates that this effort was extended to a limited number of individuals. Secondly, archaeological and ethnographic evidence suggests that mortuary practices mirror the operating status system (see Brown, 1971). Examples of this archaeologically are most often found in the appearance of grave goods accompanying certain burials. In Christian Meinarti, however, individuals did not bury any material goods with the dead. Evidence of status differentiation, however, can be determined from an alternate source. As Nubia was under the influence of the Coptic Church, an examination of the rituals governing the church proved useful. A group of rituals were found involving the burial of the dead. On these occasions, a certain passage was read depending on the age and sex of the individual involved (Meinardus, 1970:64). These passages can be taken as indications of age and sex status differentiation.

The first hypothesis tested concerned age at death and the form of burial. If age was a status factor and a determinant of the form of burial, we should expect to find an association between age at death and burial with superstructure. To test this hypothesis, the sample was divided into subadults (ages 0–20) and adults (ages 21–55) and a chi square test for association administered (see Table 1). The results of this test indicated a significant association between adults and superstructure ($\alpha = 0.001$). Further analysis suggests that the frequency of superstructures increased with the age of the individual (Figure 2, Table 2). Age, therefore, was a factor determining burial with superstructure.

Next, the association of sex of the individual and burial with superstructure was tested (see Table 3). The results of the chi square test reveal a significant association between male burials and superstructure ($\alpha = 0.001$). The possibility, however, exists that the

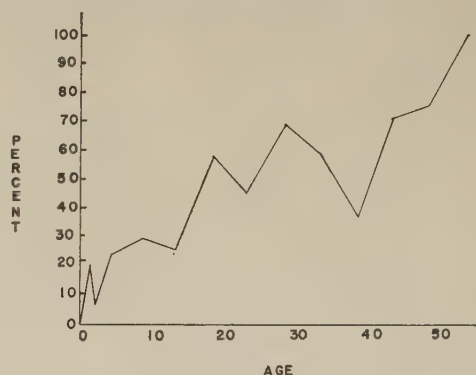
Table 1**Chi square for a association of age of individual and occurrence of superstructures at Meinarti from levels 9-7 (1050A.D.-1150A.D.)**

Provenience-age	Burials with superstructures	Burials without superstructures	Total
Levels 9-7 (1050A.D.-1150A.D.)			
Adults (over 20 years)	81	73	154
Pre-adults (under 20 years)	24	77	101
Total	105	150	255
Chi square (1 d.f.) = 2.0938*			

* Significant at greater than 0.001 level of confidence.

association of superstructure with sex is an artifact of the previously discovered association between age and burial with superstructure. In other words, if the sample of those individuals buried with superstructure contains proportionately more older males or younger females than the total population, age would bias the association with sex.

Figure 2. Percentage of burials within each age group associated with superstructures.



Thus, the significantly greater number of males could be the result of their being "old" rather than their being male. A comparison of those buried with superstructure with the total sample indicates that even though the proportion of males buried with superstructure is greater than the proportion of males in the total population, they both follow the same

Table 2**Percentage of burials in each age class associated with superstructures at Meinarti from levels 9-7 (1050A.D.-1150A.D.)**

Age class	No. burials	Burials with superstructure	
		(N)	(%)
Fetus	0	0	—
0-6 months	0	0	—
7-12 months	11	2	18
13-24 months	14	1	7
25 months-6 years	44	10	23
7-10 years	17	5	29
11-15 years	8	2	25
16-20 years	7	4	57
21-25 years	52	21	47
26-30 years	33	21	64
31-35 years	26	14	54
36-40 years	15	5	33
41-45 years	17	12	71
46-50 years	10	7	70
51-55 years	1	1	100

Table 3

Chi square values for association of sex and occurrence of superstructures at Meinarti from levels 9-7 (1050A.D.-1150A.D.)

Provenience age	Burials with superstructures	Burials without superstructures	Total
Levels 9-7			
Males	44	20	64
Females	33	43	76
Total	77	63	140

Chi square (1 d.f.) = 9.0057*

* Significant at the 0.001 level of confidence.

trends (see Figure 3). It can be concluded that the sample reflects the total population structure and that the association between sex and superstructure is valid.

Having determined age and sex as status factors, the final hypothesis was tested. This problem was approached by analyzing the mortality of the groups buried with and without superstructures. The survival curves visually depict two distinct patterns (see Figures 4 and 5) with the corresponding life tables clearly charting these differences (see Tables 4 and 5, and Figure 6).

Figure 3. Percentage of males (total population) in each age group compared with percentage of males in each age group buried with superstructure.

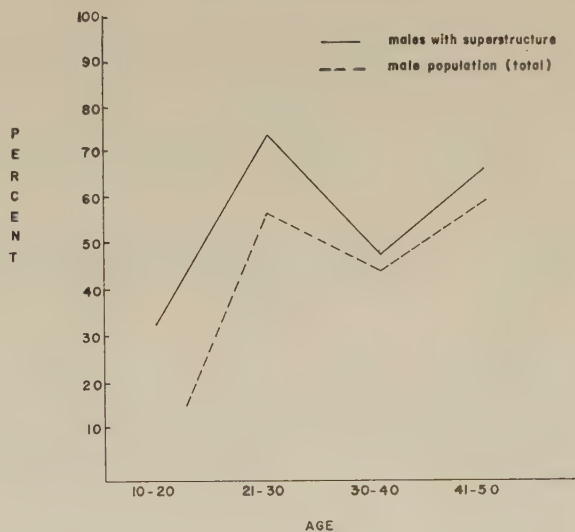


Figure 4. Percentage of persons buried with and without superstructures surviving at the end of each age interval, levels 9-7 (1050-1150A.D.).

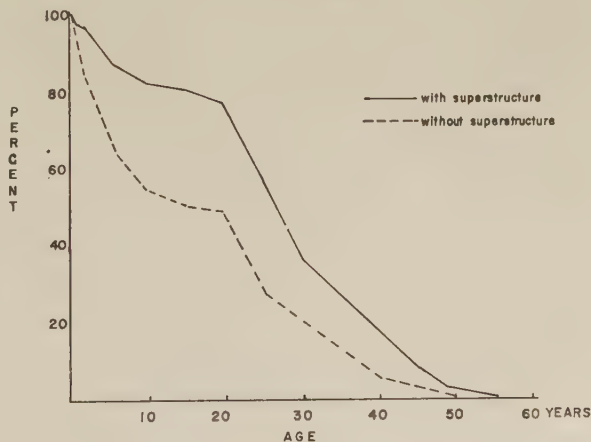
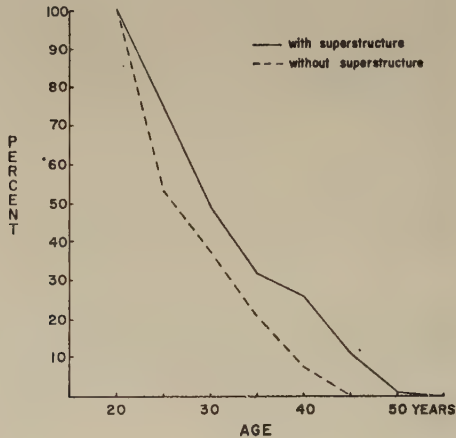


Figure 5. Percentage of adults buried with and without superstructures surviving at the end of each age interval, levels 9-7 (1050-1150A.D.).



Two alternative hypotheses have arisen in order to explain these differences.

- (1) The mortality differences are artifacts of the associations between burial type and age, and thus represent one group of persons in which status differentiation was based on age and sex.
- (2) The mortality patterns reflect biological differences in terms of varying survival rates and, therefore, indicate a status factor in addition to age and sex.

Table 4 Life table for persons buried without superstructure at Meinarti from levels 9-7 (1050A.D.-1150A.D.)

x	d ¹ x	dx	lx	qx	Lx	ex ⁰ *	ex ⁰
0-6 months	0	0	1000	0	1000	6.12	16.65
7-12 months	9	60	1000	60.0	970.0	5.13	16.15
13-24 months	13	86	940	92.6	896.5	4.43	17.15
25 months-6 years	34	228	854	267.0	739.0	3.82	18.15
7-10 years	12	80	626	128.0	585.0	4.04	19.20
11-15 years	6	40	546	73.4	525.0	3.54	17.70
16-20 years	3	20	506	39.6	495.0	2.79	13.95
21-25 years	31	205	486	422.6	382.5	1.88	9.40
26-30 years	12	80	281	284.0	241.0	1.89	9.45
31-35 years	12	80	201	398.0	161.0	1.45	7.25
36-40 years	10	67	121	555.3	87.5	1.09	5.45
41-45 years	5	33	54	611.0	32.5	0.80	4.00
46-50 years	3	21	21	1000	10.5	0.50	2.50
51-55 years	0	0	0	0	0	0	0
	150						

x The age interval.
d¹x The number of individuals dying at age x.
dx The number of individuals dying at age x based on a birth cohort of 1000.
lx The number of individuals living at age x.
qx The probability of dying at age x multiplied by 1000.
L_x The number of individuals in the life table cohort alive between ages x and x + 1.
e_x⁰* The expectation of life, or mean life-time remaining to those individuals attaining age x in age intervals.
e_x⁰ The expectation of life in years.

Table 5 Life table for persons buried with superstructure at Meinarti from levels 9-7 (1050A.D.-1150A.D.)

x	d^1x	dx	lx	qx	L_x	e_x^{0*}	e_x^0
0-6 months	0	0	1000	0	1000	8.35	24.00
7-12 months	2	18	1000	18.0	991	7.35	23.50
13-24 months	1	9	982	9.1	977	6.38	24.90
26 months-6 years	10	95	973	97.6	926	5.40	24.00
7-10 years	5	48	878	54.7	854	4.90	23.50
11-15 years	2	18	830	21.7	821	4.22	21.10
16-20 years	4	38	812	46.8	793	3.19	15.95
21-25 years	21	199	774	257.0	697	2.43	12.15
26-30 years	21	199	575	346.0	476	2.08	10.40
31-35 years	14	130	376	346.0	311	1.39	9.45
36-40 years	5	48	246	195.0	222	1.69	8.35
41-45 years	12	117	198	590.0	139	0.96	4.80
46-50 years	7	70	81	864.0	46	0.63	3.15
51-55 years	1	11	11	1000	55	0.50	2.50
	107						

For abbreviations see Table 4.

On examination of the mortality data, the second hypothesis becomes most probable. Despite the positive associations which exist between burial with superstructures, increasing age and males; 24% of preadults (less than 20 years of age) and 43% of females in the population are buried with superstructure and, conversely, 47% of adults (greater than 20 years of age) and 37% of adult males of the population are buried without superstructure.

	Burials with superstructure (%)	Burials without superstructure (%)	Total (%)
Adults	53	47	100
Subadults	24	76	100
Adult Males	67	33	100
Adult Females	43	57	100

These percentages, though still upholding the previously established association, indicate that age and sex do not totally explain the distribution of the superstructures, and

Figure 6. Life expectancy for each age group for individuals buried with and without superstructures.

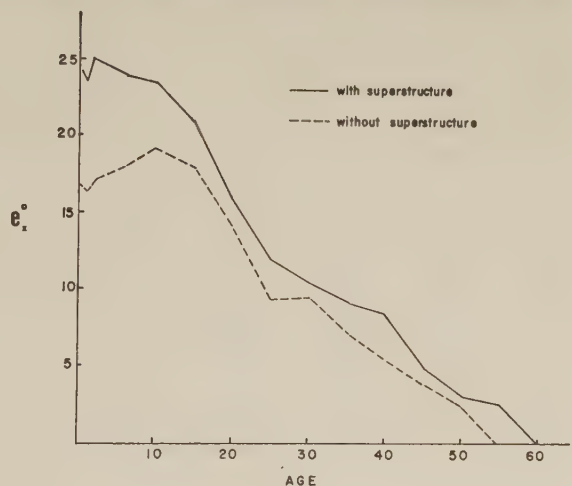
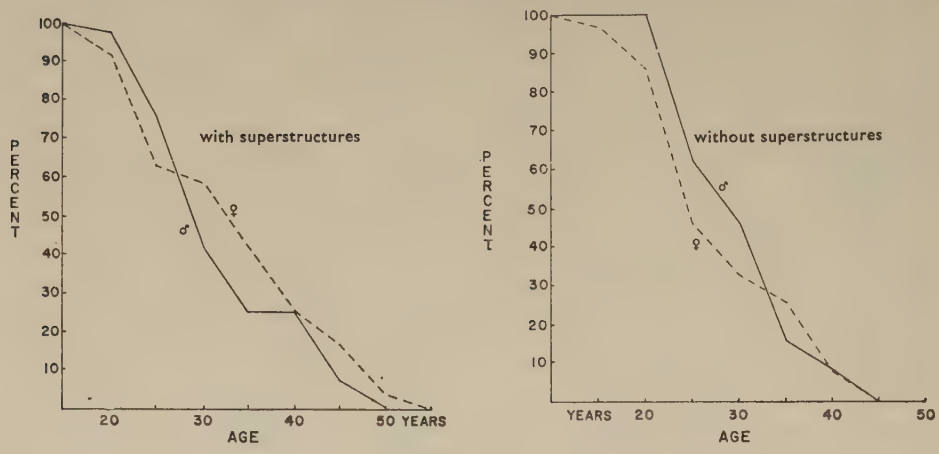


Figure 7. Percentage of males and females surviving at the end of each age interval for individuals buried with and without superstructures.



that an additional status factor exists. Some distinction, for example, is indicated between those males of the same age buried with superstructure and those buried without them.

Analysis of the survival curves of males and females of the two groups further supports the second hypothesis (see Figure 7). These curves follow the expected mortality pattern of non-industrial societies with initially high female mortality (as a result of death at childbirth) and a subsequent rise in male mortality. The fact that these distributions follow the expected mortality patterns for agricultural populations indicates that they represent distinct groups in terms of mortality rather than one group differentiated only by age and sex status. This is not to say that at birth an individual was assigned to a specific status group but rather, those individuals who were buried with superstructures as a result of their status within the society had a lower mortality rate than those buried without structures. The differences in mortality between the groups, therefore, represent

Figure 8. Percentage of persons surviving at the end of each age interval, levels 9-8 (1050-1100 A.D.) and 7 (1100-1150A.D.).

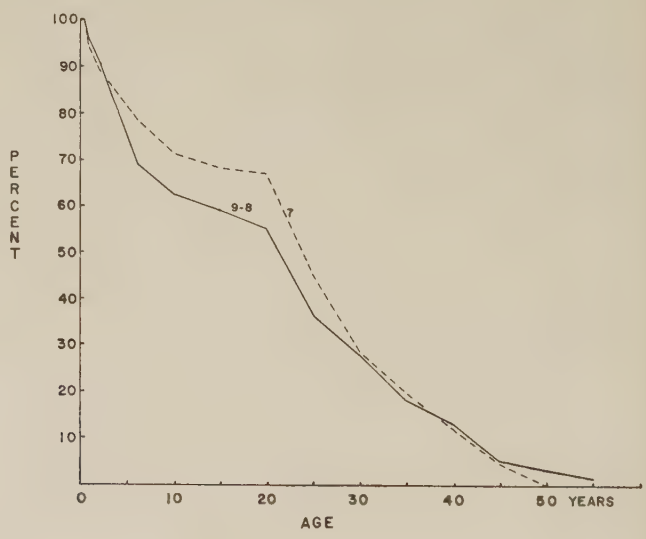


Table 6

Life table for levels 9-8 (1050A.D.-1100A.D.) at Meinarti

<i>x</i>	d^1x	dx	lx	q_x	L_x	e_x^{0*}	e_x^0
0-6 months	0	0	1000	0	1000	6.71	19.55
7-12 months	5	35	1000	35.0	982.5	5.71	19.05
13-24 months	8	56	965	58.0	937.0	4.90	19.50
2-6 years	32	226	909	249.0	796.0	4.17	19.85
7-10 years	10	71	683	104.0	647.5	4.38	20.90
11-15 years	4	29	612	47.4	597.5	3.83	19.15
16-20 years	6	42	583	72.0	562.0	3.00	15.00
21-25 years	28	192	541	355.0	445.0	2.19	10.95
26-30 years	13	90	349	258.0	304.0	2.13	10.65
31-35 years	14	99	259	382.0	209.5	1.69	8.45
36-40 years	7	50	160	312.0	135.0	1.43	7.15
41-45 years	11	80	110	727.0	70.0	0.86	4.30
46-50 years	3	21	30	667.0	20.0	0.83	4.15
51-55 years	1	7	9	1000	5.0	0.50	2.50
	142						

For abbreviations see Table 4.

biological differences in terms of survival and thus indicate an additional status factor which affected the mortality of the persons in the village.

The second problem dealt with was the relationship between the mortality and settlement patterns for levels 9-8, 7 and 6-4 (see Swedlund & Armelagos, 1968). As previously discussed, Adams (1968:190) has stated that archaeological evidence indicates levels 9-8 as a period of village growth, and level 7 as a period of decline at Meinarti. A comparison of the survival curves for these two levels apparently indicates level 7 as having a lower mortality than levels 9-8 (see Figure 8). Life table analysis, however, indicates that although the life expectancy of level 7 for subadults (ages 0-20) is greater than levels 9-8 (with the probability of dying correspondingly lower), the reverse is true for the adult segment of the population (see Tables 6 and 7, Figure 9). Truncation of the subadult portion of the survival curve supports this analysis (see Figure 10), thus revealing the initial survival curve (Figure 8) to be influenced by the apparent lower mortality of the subadult age groups.

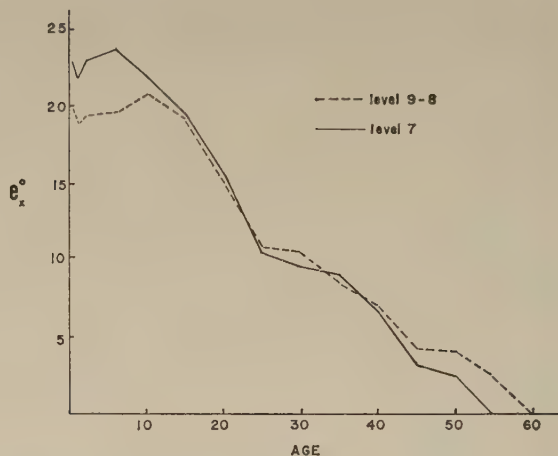
Table 7

Life table for level 7 (1100A.D.-1150A.D.) at Meinarti

<i>x</i>	d^1x	dx	lx	q_x	L_x	e_x^{0*}	e_x^0
0-6 months	0	0	1000	0	1000	7.30	22.50
7-12 months	5	48	1000	48.0	976.0	6.30	22.00
13-24 months	6	57	952	59.9	923.5	5.59	22.95
26 months-6 years	12	115	895	12.8	837.5	4.92	23.60
7-10 years	6	58	780	74.3	751.0	4.58	21.90
11-15 years	4	38	722	52.6	703.0	3.91	19.55
16-20 years	1	10	684	14.6	679.0	3.10	15.50
21-25 years	23	220	674	326.0	564.0	2.13	10.65
26-30 years	18	172	454	379.0	368.0	1.93	9.65
31-35 years	9	85	282	301.0	239.5	1.80	9.00
36-40 years	8	74	197	376.0	160.0	1.37	6.85
41-45 years	8	74	123	602.0	86.0	0.89	4.45
46-50 years	5	49	49	1000	24.5	0.50	2.50
51-55 years	0	0	0	0	0	0	0
	105						

For abbreviations see Table 4.

Figure 9. Life expectancy for each age group, levels 9-8 (1050-1100A.D.) and level 7 (1100-1150A.D.).



Furthermore, analysis of the adult sex ratio reveals level 7 to have the lowest percentage of females in the Meinarti series (33 % in comparison to 61 % for levels 9-8, for example, see Table 8). It can, therefore, be inferred that the reduction of the number of subadults, and the resulting low mortality revealed by the survival curves and life tables for this age group, is a result of a decrease in the number of births. In other words, the scarcity of subadult burials can be attributed to their absence from the community rather than their having survived to an older age.

The low mortality for level 7 subadults as indicated by life expectancy, probability of dying and the survival curves, appears not to be a true reflection of the survival. Truncation of this portion of the distribution as facilitated by the life table is necessary to get a more accurate picture of the mortality. The results of this show the mortality of levels 9-8 to be lower than level 7, lending support to Adam's analysis.

Although the burial data from levels 6-4 is somewhat incomplete (superstructures have been washed away), a comparison of the available mortality statistics and those of levels 9-7 provides some useful information. The survival curves for these two periods indicate the mortality rate of levels 9-7 to be substantially lower than the mortality of

Figure 10. Percentage of adults surviving at the end of each age interval, levels 9-8 (1050-1100 A.D.) and 7 (1100-1150A.D.)

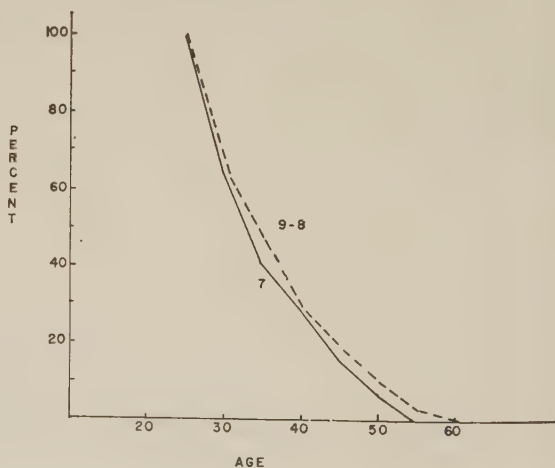


Table 8

Percentage of males and females at Meinarti

Levels 9-4
(1050A.D.-1300A.D.)

	<i>N</i>	%
Male	79	47
Female	89	53

Levels 9-7
(1050A.D.-1100A.D.)

	<i>N</i>	%
Male	64	46
Female	74	54

Levels 9-8
(1050A.D.-1100A.D.)

	<i>N</i>	%
Male	25	39
Female	39	61

Level 7
(1100A.D.-1150A.D.)

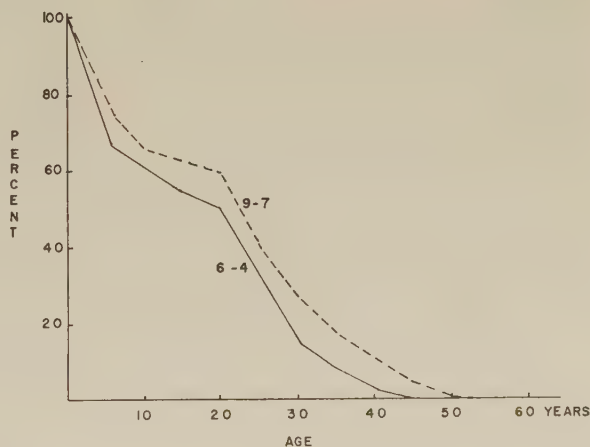
	<i>N</i>	%
Male	39	67
Female	29	33

Levels 6-4
(1150A.D.-1300A.D.)

	<i>N</i>	%
Male	14	48
Female	15	52

levels 6-4 (see Figure 11). This difference is substantiated by the life table analysis of the two levels (see Tables 9 and 10). Life expectancy for levels 9-7 is consistently and substantially greater than for levels 6-4 and the probability of dying consistently lower. This analysis supports the evidence presented by Adams indicating levels 6-4 as a period of further decline in the village.

Figure 11. Percentage of persons surviving at the end of each age interval, levels 9-7 (1050-1150 A.D.) and 6-4 (1150-1300 A.D.) at Meinarti.



5. Concluding Remarks

We have attempted to relate changes in settlement patterns and several demographic parameters of a population. It was noted that such analysis has to be defined within the delimited spatial and temporal framework of the archaeological settlement. Within this context, demographic and archaeological analysis can be used as a complementary means of testing hypotheses concerning the mortality patterns of the group under study.

Table 9 Life table for levels 9-7 (1050A.D.-1150A.D.) at Meinarti

x	d^1x	dx	lx	q_x	L_x	e_x^{0*}	e_x^0
0-6 months	0	0	1000	0	1000	7.10	21.50
7-12 months	10	39	1000	39.0	980.5	6.10	21.00
13-24 months	15	59	961	61.4	931.5	5.40	22.00
2-6 years	44	172	902	190.7	816.0	4.55	21.75
7-10 years	17	66	730	90.4	697.0	4.50	21.50
11-15 years	8	32	664	48.2	648.0	3.90	19.50
16-20 years	7	28	632	44.3	618.0	3.07	15.35
21-25 years	50	198	604	327.8	505.0	2.19	10.95
26-30 years	33	131	406	322.6	340.5	2.02	10.10
31-35 years	25	99	275	360.0	225.5	1.74	8.70
36-40 years	15	57	176	323.9	147.5	1.45	7.25
41-45 years	19	73	119	613.4	82.5	0.90	4.50
46-50 years	11	41	46	891.3	25.5	0.59	2.95
51-55 years	1	5	5	1000	2.5	0.50	2.00
	255						

For abbreviations see Table 4.

Table 10 Life table for levels 6-4 (1150A.D.-1300A.D.) at Meinarti

x	d^1x	dx	lx	q_x	L_x	e_x^{0*}	e_x^0
0-6 months	1	14	1000	14.00	993.0	6.25	17.25
7-12 months	5	68	986	69.0	936.0	5.33	17.15
13-24 months	1	14	918	15.2	915.5	4.70	18.50
2-6 years	17	233	904	257.7	787.5	3.76	17.80
7-10 years	4	55	671	82.00	643.5	3.90	18.50
11-15 years	3	41	616	66.5	595.5	3.20	16.00
16-20 years	5	68	575	118.3	541.0	2.40	12.00
21-25 years	13	180	507	355.0	471.0	1.65	8.25
26-30 years	13	180	327	550.4	237.0	1.29	6.45
31-35 years	5	66	147	449.0	114.0	1.26	6.30
36-40 years	4	49	81	604.9	56.5	0.89	4.45
41-45 years	2	32	32	1000	16.0	0.50	2.5
46-50 years	0	0	0	0	0	0	0
	73						

For abbreviations see Table 4.

Four factors qualify Meinarti as a good working example for this type of analysis:

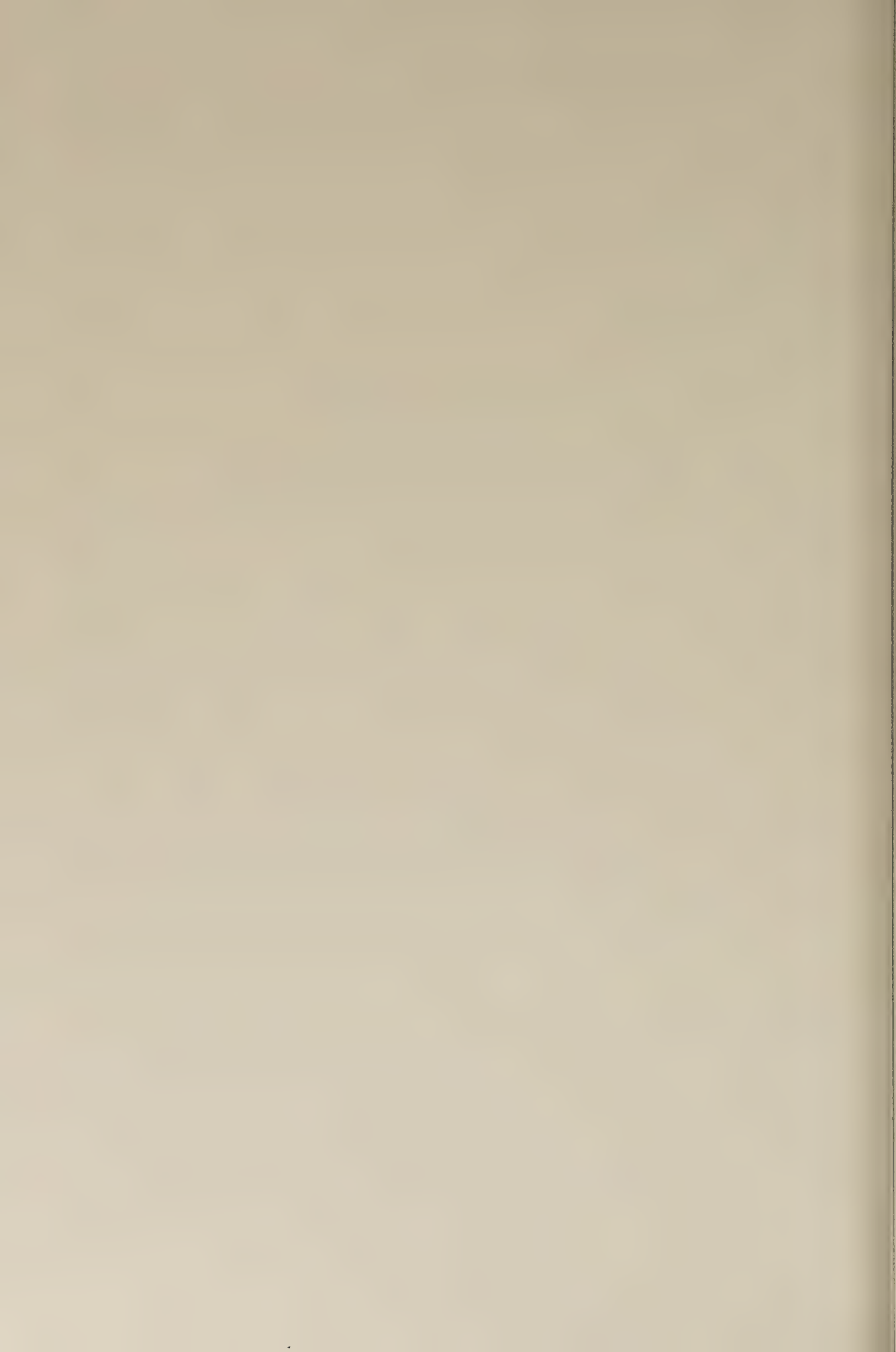
- (1) Clear spatial and temporal definition.
- (2) Correlated stratigraphy between the village and the stratified cemetery.
- (3) Evidence that the same group of people inhabited the site throughout its occupation and no indications of migrations.
- (4) Complete excavation of the cemetery.

The two problems discussed illustrate the manner in which populational and archaeological analysis can be used in a complementary manner. In the analysis of the Meinarti mortality data, sex, age and an additional factor were shown to be determinants of status. Furthermore, it was demonstrated that the mortality patterns of the groups with and without superstructures reflect biological differences in terms of survival.

In the second problem, mortality analysis was used to test hypotheses put forth by Adams concerning the growth and decline of the village of Meinarti during the periods represented by levels 9-8, 7 and 6-4.

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T. Sharma
G. S. Garg

Cytogenetics Laboratory,
Department of Zoology,
Banaras Hindu University
Varanasi-221005, India

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Restrictive Localization of Centromeric Heterochromatin (C-bands) in *Presbytis e. entellus* (Dufresne) as compared to *Macaca mulatta* (Zimmerman)

C-bands are observed in the centromeric regions of only three pairs of autosomes and the distal portion of the small acrocentric Y in a total complement of 44 chromosomes of a male *Presbytis e. entellus*. Simultaneously treated slides of a Rhesus monkey, however, have C-bands in all the 42 chromosomes. The lack of C-bands may be due to (1) absence of highly repetitive DNA in the centromeric region of certain chromosomes or (2) presence of minute quantity of such DNA which is imperceptible or (3) different types of centromeric heterochromatin with a varying degree of repetition of DNA sequences all of which do not react in similar manner to various techniques employed at present. It is hypothesized that the centromeric heterochromatin rich in satellite DNA helps in withstanding the force of excessive coiling of chromosomes at the centromere to facilitate the functioning of the genes for microtubular protein during cell division when other genes are rendered inactive due to compactness of chromosomes.

1. Introduction

Pardue & Gall (1970) and Jones (1970) discovered that the satellite DNA in the mouse are localized at the centromeric regions of chromosomes. This was demonstrated by *in situ* DNA-RNA or DNA-DNA hybridization technique in cytological preparations. In their preparations Pardue & Gall had also noted that the centromeric regions of the chromosomes were stained more intensely with Giemsa. Arrighi & Hsu (1971) further developed the Giemsa staining procedure based on denaturation and reassociation technique for differential staining of centromeric heterochromatin. Yunis *et al.* (1971) also reported staining of satellite DNA localized at the centromeric region by cytochemical procedure. Hilwig & Gropp (1972) found a new fluorochrome which brightly fluoresced the centromeric heterochromatin specifically.

The characteristic and highly consistent differential staining behaviour of the constitutive heterochromatin revealed by simple cytological procedures provided additional criterion for identification of chromosomes. This constitutive heterochromatin is known as C-band (Paris Conference, 1971). The localization of highly repetitive satellite DNA at the centromeric regions created considerable interest for the possible involvement in some function of this species of DNA (Walker, Flamm & McLaren, 1969; Walker, 1971) which is apparently nontranscriptional (Flamm, Walker & McCallum, 1969).

A number of investigations employing similar cytochemical procedures or with some modifications on human and other mammalian chromosomes revealed that all the autosomes and the X, but not the Y, except that of the Rhesus monkey, have characteristic band of constitutive heterochromatin at the centromeric region. The Y has C-band in the distal portion of the long arm instead, and a very few autosomes in certain species have interstitial C-bands (Hsu & Arrighi, 1971; Bianchi & Ayres, 1971*a,b*; Chen & Ruddle, 1971; Sumner, Evans & Buckland, 1971; Sumner, 1972; Cooper & Hsu, 1972; Hansen, 1973; Pathak, Hsu & Utakaji, 1973). In a few mammals, however, lack of

distinct C-bands in some of the autosomes (Unakul & Hsu, 1972; Kakati & Sinha, 1972) or in all the autosomes (Sinha, Kakati & Pathak, 1972) has been observed. We describe in this paper a Primate, popularly known as the Indian common Langur, possessing C-bands in only a few chromosomes of the complement. Simultaneous treatment of the chromosomes of a female Rhesus monkey has however revealed C-bands in all the chromosomes. An abstract of this finding has been published recently (Sharma & Garg, 1973).

2. Materials and Methods

One male Indian common Langur, *Presbytis e. entellus* (Dufresne) was captured on the foothills of Eastern Nepal (Damak). A female Rhesus monkey, *Macaca mulatta* (Zimmerman) was captured at Varanasi in India. The chromosome preparations were made from bone marrow and spleen short-term cultures following the usual air-drying procedure.

For C-band staining the method of Schnedl (1971) was adopted with slight modifications. In brief, the procedure was as follows:

- (1) Slides were treated for 90–150 sec in 0.07 N-NaOH at 21°C and then quickly rinsed in 70 % and 95 % ethyl alcohol.
- (2) After thorough rinsing the slides were incubated in Sörensen buffer for 32 hr at 54°C.
- (3) The slides were then rinsed once in absolute ethyl alcohol and air dried.
- (4) Finally the slides were stained in Giemsa (BDH) at pH 6.9 and mounted in DPX.

3. Observations

In *Presbytis e. entellus* $2n = 44$ (Plate 1), as reported by Sharma & Kakati (1967), and in *Macaca mulatta* $2n = 42$ (Plate 4), as reported earlier by many workers, were observed.

The result of C-band staining was very interesting. In *Presbytis e. entellus* all the chromosomes of the complement did not possess centromeric heterochromatin (Plates 2 and 3). The C-band was present in the centromeric region of only 3 pairs of autosomes, one metacentric, one submetacentric and one acrocentric. The X chromosome did not have any C-band but the distal region of the acrocentric Y had intensely stained characteristic band. The treatment of slides to different durations for denaturation in NaOH had either shown C-bands in the three pairs of autosomes and the Y only or none at all. This peculiarity was observed to be consistent in all the 149 metaphases exhibiting the C-band reaction.

The simultaneously treated slides of *M. mulatta* showed an entirely different picture. All the chromosomes, including the X, had intensely stained C-band in the centromeric regions (Plate 4). The observation on the C-bands of the Rhesus monkey published recently by Stock & Hsu (1973) is identical to our finding (Sharma & Garg, 1973).

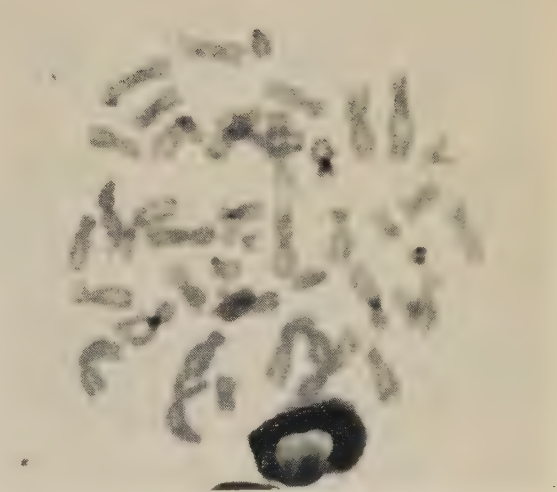
4. Discussion

A number of speculative roles of satellite DNA have been suggested (see Flamm, 1972). The localization of highly repetitive satellite DNA at the centromeric region has obviously

Plate 1. Karyotype of the male *Presbytis e. entellus*. ($\times 1600$.)



Plate 2. Metaphase of *Pres. bytis entellus* showing C-bands in 3 pairs of autosomes and the Y. ($\times 1600$.)



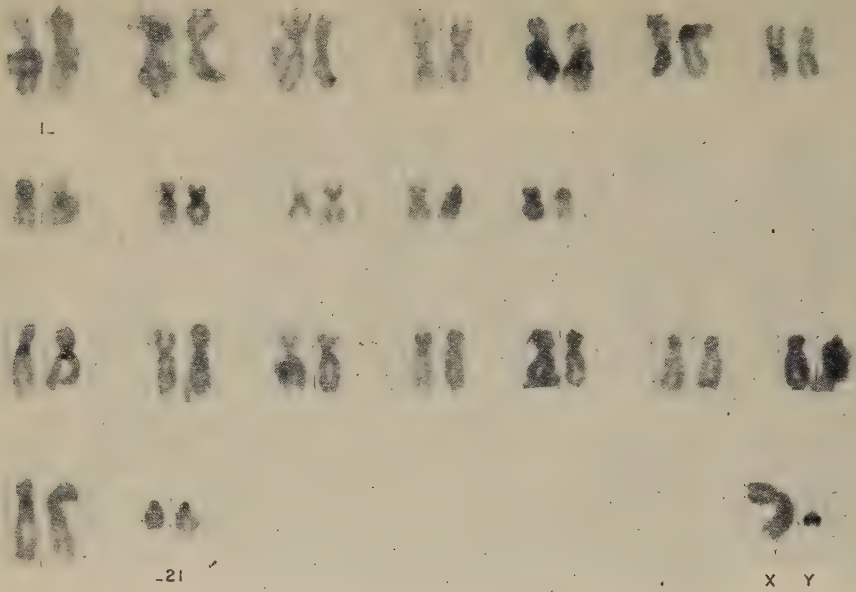
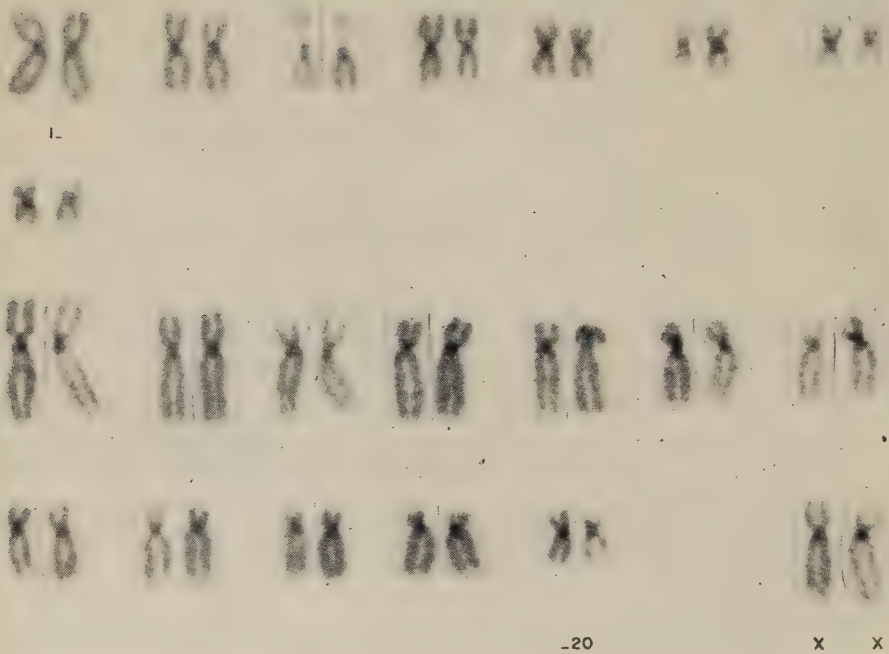


Plate 4. Karyotype of the female *Macaca mulatta*. All the chromosomes of the complement have C-bands. ($\times 1600$.)



led people to presume its probable involvement in the centromeric function. Walker (1971) has suggested that the quantity of heterochromatin adjacent to the centromere might confer a selective advantage on the chromosome by contributing some strength to the centromere. Walker cited the work of Lindsley & Novitski (1958) on *Drosophila* who had demonstrated experimentally that the firmness of attachment of the spindle to the centromere depended on the quantity of heterochromatin adjacent to the centromere, and the work of Rhoades (1952) on neocentromeric activity of heterochromatic knob of maize in support of his assumption. On the basis of the same evidence, Brown (1966) had also inferred earlier that the heterochromatin probably contributed directly in influencing chromosome orientation or centromere potency. Since the effects occurred late in the division cycle Brown hypothesized that the effects might reflect the physical state of the regions adjacent to the centromere rather than influences analogous to typical gene function. Craig-Holmes & Shaw (1971) have, on the other hand, guessed that possibly the centromeric heterochromatin codes for microtubule formation and assembly. It becomes extremely difficult at present to agree to such proposition since no convincing evidence is available in support of transcriptional activity of satellite DNA (see Flamm, 1972). It is no less difficult to envisage how exactly the influences as suggested by Brown (1966) and Walker (1971) act.

The polymorphism of centromeric heterochromatin observed in Man (Craig-Holmes & Shaw, 1971), in guinea pig (Bianchi & Ayres, 1971) and in the mouse (Forejt, 1973) indicates that obviously quantitative variation is not critical. The localization of centromeric heterochromatin in only a few pairs of chromosomes observed in Indian common Langur is rather intriguing. We have also observed in a rodent only a few pairs of the complement having centromeric heterochromatin (Sharma & Garg, unpublished). Similarly, lack of C-bands in a few chromosomes (Unakul & Hsu, 1972; Kakati & Sinha, 1972) or in all the autosomes (Sinha, Kakati & Pathak, 1972) have also been reported. Such a disparity undermines the role of the highly repetitive DNA rich constitutive heterochromatin localized at the centromeric region. However, even when only a few chromosomes of the complement possess centromeric heterochromatin it is present in both the homologues. This apparently suggests that selection favours either presence of centromeric heterochromatin in both the homologues or none at all.

The lack of centromeric heterochromatin (C-bands) in certain chromosomes as observed in the present investigation may be due to either absence of highly repetitive DNA in them or presence of a minute quantity which is imperceptible with the procedures employed. There may even be different types of centromeric heterochromatin depending on the degree of repetition of DNA sequences all of which do not react in similar ways to various techniques available at present. Unfortunately, the mechanism of banding is not understood and therefore, it becomes difficult to draw any conclusion. Furthermore, the specific mechanism of origin of satellite DNA is also not known. Different types of highly repetitive sequences have been reported even within a species, and they appear and vanish rather rapidly in the course of evolution (Flamm, 1972). The heterogeneity, high rate of turnover and lack of transcriptional activity indicate that the highly repetitive DNA sequences are only structural components. The centromeric heterochromatin rich in such DNA may act as protector of genes for microtubular protein which have remained conserved throughout the evolutionary history of eukaryotes (Ohno, 1970) as suggested by Yunis & Yasmin (1972) or as well it helps in withstanding the force of excessive coiling of chromosomes at the centromere so that the genes for microtubular protein may

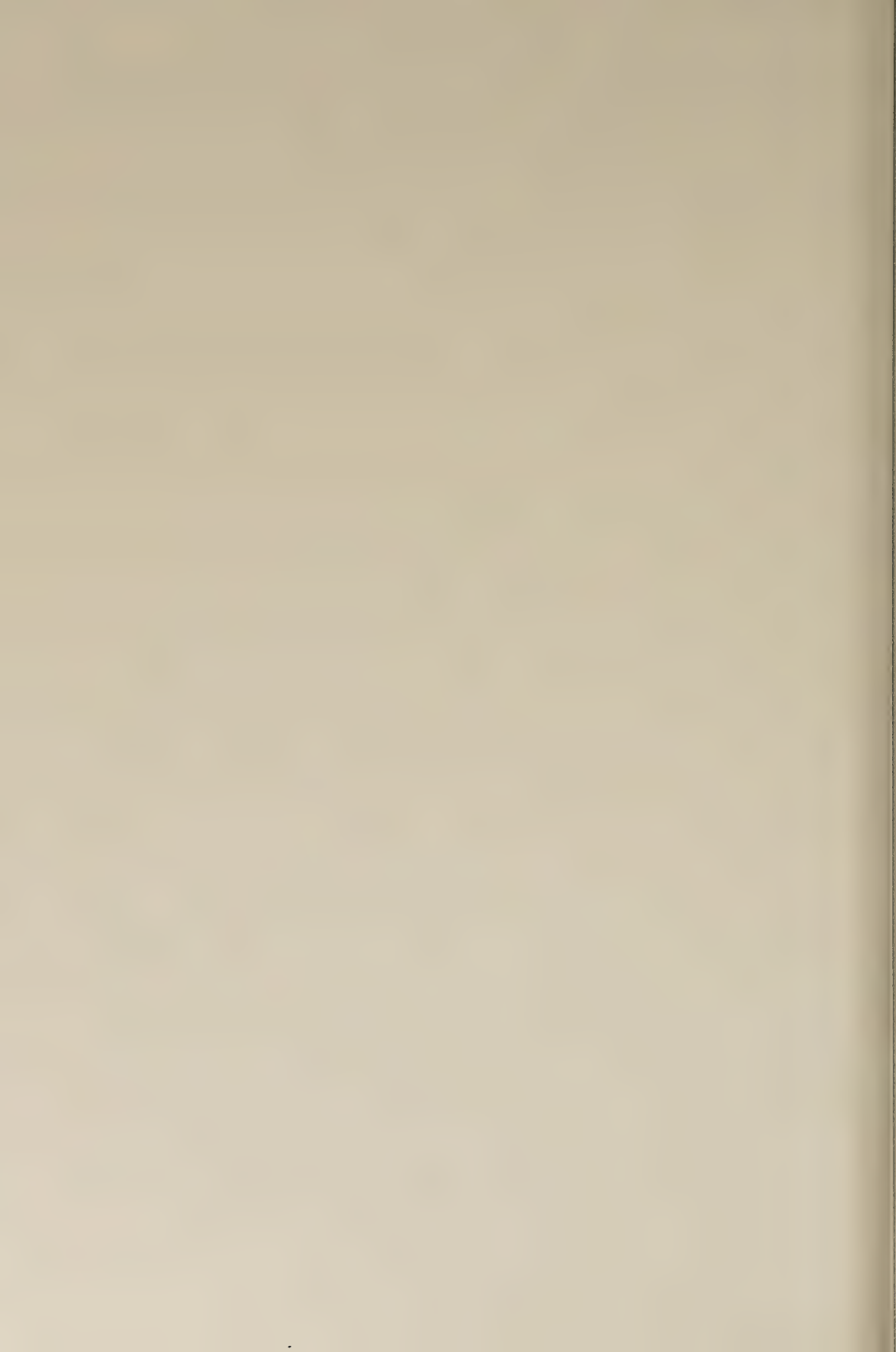
function properly during cell division when other genes are rendered inactive due to a great degree of compactness of chromosome arms. An analogous situation may exist for nucleolus organizing secondary constrictions.

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Institute of Anthropology,
Via Accademia Albertina 17,
University of Turin, 10123
Turin, Italy

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Following the lists of numerical data on the chromosomes of the Prosimians and of the Old World Primates, published in this journal [Journal of Human Evolution 2(4)], here is a list concerning the chromosome information on the New World Primates.

Taxa*	2n	S-M	A	X	Y	References
1.1 Callithrix						
1. C. argentata	44	28-32	10-14	S	M-A	22, 35, 39, 46
2. C. humeralifer	44-46	30-32-34	10-14	S	S-M-A	3, 4, 17, 22, 36
3. C. jacchus	44-46	32-(34)	10-12	S	A	6, 7, 9, 10, 13, 14, 15, 22, 43, 46
1.2. Cebuella						
1. C. pygmaea	44	32	10	S	A	7, 9, 10, 19, 22, 43
1.3. Leontideus						
1. L. rosalia	46	32-(34)	(10)-12	S	M	6, 7, 8, 9, 10
2. L. chrysomelas						
3. L. chrysopygus						
1.4. Saguinus						
1. S. tamarin	46					8
2. S. midas						
3. S. fuscicollis	46	30-34	10-14	S	M	4, 22, 23, 37
4. S. graellsii						
5. S. nigricollis	46	30-(32)-(34)	(10)-(12)-14	S	M	7, 8, 9, 43
6. S. imperator						
7. S. mystax	46	30	14	S	M	8, 11, 43
8. S. labiatus						
9. S. geoffroyi						
10. S. oedipus	46	30-(32)-(34)	(10)-(12)-14	S-M	M-A	7, 8, 9, 13, 22, 38, 39, 45, 46
11. S. leucopus	46	30	14	S	S	8, 11, 39
12. S. inustus						
13. S. bicolor						
14. S. martinsi						
2.1. Callimico						
1. C. goeldii	48	28-32	16-18	S	A	3, 4, 22, 39, 46
3.1. Aotes						
1. A. trivirgatus	49-50-51-52-53-54	18-20-2122-30-32-34	18-20-22-25-28-30-32	S-M	S-M-A	5, 12, 13, 14, 15, 17, 18, 23, 40, 42, 45, 46, 47
3.2. Callicebus						
1. C. cupreus	46-50?	20-22	24-26	S	S-M-(A)	3, 17, 24, 46
2. C. torquatus	20	10	10	—	—	17, 24
3. C. gigot						
3.3. Pithecia						
1. P. pithecia	46-(48)	(18)	(28)	(S)	(S)	16, 48
2. P. monachus						
3.4. Chiropotes						
1. C. satanas	54	24	30	—	—	46
2. C. albinasa						

Taxa*	2n	S-M	A	X	Y	References
3.5. Cacajao						
1. <i>C. calvus</i>						
2. <i>C. rubicundus</i>	45-46	20-22	24-25	—	—	16, 17, 46
3. <i>C. melanocephalus</i>						
3.6. Alouatta						
1. <i>A. villosa</i>	53?					33
2. <i>A. fusca</i>	50	20	28	S	A	40
3. <i>A. seniculus</i>	44	12-(16)	(26)-30	(A)	(S-M)	1, 17
4. <i>A. belzebul</i>						
5. <i>A. caraja</i>	52	20	30	S	A	17, 25, 26, 28, 31
3.7. Saimiri						
1. <i>S. sciurea</i>	44	28-30-32	10-12-14	S	A	3, 13, 14, 15, 17, 24, 32, 41, 44, 45, 46
2. <i>S. oerstedii</i>						
3.8. Cebus						
1. <i>C. apella</i>	54	26	26	S-A	A	3, 13, 14, 15, 16
2. <i>C. capucinus</i>	52-54	18-20- 24-26	26-28- 30-34	S-A	A	3, 13, 14, 15, 16, 17, 27, 29
3. <i>C. albifrons</i>	52-54	18-20	32	S	A	29, 30, 40, 46
4. <i>C. nigrivittatus</i>						
3.9. Ateles						
1. <i>A. paniscus</i>	34	30	2	S-M	A	3, 13, 16, 40, 46
2. <i>A. fusciceps</i>	34	30	2	S	S	44
3. <i>A. belzebuth</i>	34	30	2	M	A	3, 16, 46
4. <i>A. geoffroyi</i>	34	30	2	S-M	S-M-A	3, 16, 20, 24, 34
3.10. Brachyteles						
1. <i>B. arachnoides</i>	34					14, 15
3.11. Lagothrix						
1. <i>L. lagotricha</i>	62	30	30	S	A	1, 2, 21, 40, 46
2. <i>L. flavicauda</i>						

* The code numbers for the species are the ones used in A. B. Chiarelli (1972). *Taxonomic Atlas of Living Primates*. London: Academic Press.

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R. Lavocat

*Laboratoire de Paléontologie des
Vertébrés,
Institut de Montpellier de l'Ecole
Pratique des Hautes Etudes, France*

Received 9 March 1974 and
accepted 22 March 1974

The Interrelationships Between the African and South American Rodents and Their Bearing on the Problem of the Origin of South American Monkeys

The first presence of Primates in South American Oligocene, at the same time as the Rodents, suggests a similar history. The anatomical similarities between African (Phiomorpha) and South American (Caviomorpha) rodents cannot satisfactorily be explained without direct relationships. As a consequence of continental drift, the migration by rafts, if not easy, was certainly possible in early Tertiary. The same is true for Primates.

It may be rather surprising to read in a journal devoted to human evolution a paper on rodents. This contribution is justified by the fact that the study of rodents can provide excellent arguments in favour of the African origin of the South American Primates.

We recently learned (Hoffstetter, 1969) that the Primates were present in South America during the Oligocene (Deseadian), as were the caviomorpha rodents. As long as the period of introduction of these two groups seemed to be entirely different, the Primates being known only since the Miocene, there was no particular reason to relate one group to the other. But now, there are certainly good reasons to suggest that the migration process must have been the same for the two orders. So, it is certainly important to pay particular attention to the rodents, since they have the important advantage of being known by a great number of much more complete samples.

One fact is absolutely certain, whatever its interpretation: the anatomical similarities and even identities between the South American Caviomorpha and Old World Phiomorpha are evident and numerous, so much so that already a century ago the best specialists of the order, for example Tullberg (1899), naturally associated them in the same systematical unit. Of course, in a stabilist understanding of the continents, such a conclusion had to face enormous problems. Obviously, it was very difficult to imagine which migration route could explain the close relationships of so widely distant faunas. The anatomical arguments are nevertheless so strong that Matthew (1915) himself, making a remarkable exception to his general theory, definitely admitted and published the idea of a direct migration from Africa to South America through the Atlantic, notwithstanding the difficulties of crossing several thousand kilometers of ocean.

These difficulties are so evident that Wood (1950) published his important paper "Porcupines, paleogeography and parallelism" in which, reviewing the various theoretical possibilities of a migration from Africa and or Asia toward South America, he concluded that none could be taken seriously. Indeed, the only acceptable explanation of the evident similarities between the Caviomorpha and the then called Hystricomorpha was a strong but pure parallelism.

Previously (Wood, 1949) he had developed the idea that the structure of the tooth of the two groups was entirely different in its origin, the Hystricomorpha (now Phiomorpha) teeth being pentalphodont, while those of the Caviomorpha were initially strictly tetralphodont. In his opinion, the fifth crest present in some genera, which was then morphologically pentalphodont, was a neoformation, called by him neoloph. If

accepted, such a difference appeared as clearly excluding a common origin and strongly arguing in favour of parallelism. This position is explained in great detail by Wood & Patterson (1959) in their study of the Deseadan rodents of Patagonia, and they conclude that the Caviomorpha were introduced in South America, shortly before Oligocene, by a migration originating in North America, and not in Africa. We must here note the very important fact that, if coming from North America, these rodents had nevertheless to cross an important sea.

More recently, Wood (1968) in his study of the Fayum Oligocene rodents of Egypt retains the same general position, accepting a typically pentadelphodont interpretation of all the Phiomorpha teeth, even of *Gaudeamus*.

Until very recently, these opinions of Wood were shared by myself completely, and I have published in the same direction. What literally forced me to entirely reverse my opinion was the study of the whole of the rodent fauna of the Ancient and Middle Tertiary of Africa, recently published, for the Early Miocene (Lavocat, 1973). It is very important to point out that this early Miocene fauna is one of the most complete possible, consisting of several hundred samples. Not only teeth and teeth rows, but the complete skulls, beautifully preserved, of several genera of Miocene Phiomorpha; also, the skeleton of two of these genera.

The study of the whole, shows that the identity of the structures with those of the Caviomorpha is so complete and fundamental that it seems entirely impossible to explain it by a mere parallelism. Only direct relationships can satisfactorily explain such structural identities. Recently an extensive analysis (not yet published) of the osteology of the rodent's skull gave me the opportunity to recognize several fundamental structures. The observation shows that most, if not all, of these structures are not intrinsically connected between themselves, since we find them separately within different groups. We know, for example, by the European Eo-Oligocene Theridomorpha, that the hystricomorph character of the infra-orbital foramen is not essentially connected with the hystricognath character of the mandible, and not with the perforated character of the pterygoid fossa, and so on. In such a situation, it is highly improbable that the various important features of the Phiomorpha skull could be all found identically interconnected in the Caviomorpha skull only by chance. But it is a fact that this identity exists, not only for the characters studied by Tullberg, but for several others, some of them of considerable importance, the middle ear region for example. This structural identity can be demonstrated as early as the Oligocene, as is shown by the skulls of three different genera of the Deseadian of Bolivia, the teeth of which are already published (Hoffstetter & Lavocat, 1970). Moreover, I think that the opinions of Wood according to which there are basic plan differences between Phiomorpha and Caviomorpha teeth is not supported by the comparative study of Miocene and Oligocene teeth of the Phiomorpha, and of the Caviomorpha, specially of those from the Bolivian Oligocene.

The structural identity is true, not only for the skull and the teeth, but also for the post-cranial skeleton, for the muscles, the urethral part, the foetal membranes etc. Matthew thought it necessary to accept the transatlantic crossing, notwithstanding the very high improbability, according to the scientific knowledge in 1915. Now, there is no such dilemma. Continental drift is a scientifically recognised fact, and there is now no doubt that, before Oligocene, the distance between Africa and South America was much shorter, specially if we consider that for a long time the North Eastern part of South America was sliding, parallel to the African coast west of the Gulf of Guinea. Distinguished

geophysicists assume that in the Middle Eocene period the South American Eastern Cape and the part of African coast where Dakar now stands were approximately on the same meridian line.

It is nearly certain that the equatorial sea current from Africa toward South America already existed, and quite probably at least a part of it, was crossing, toward the Pacific, the then existing sea channel between the two Americas. In such a situation, while evidently helping travel from Africa to South America, the sea current was at the same time strongly preventing connections between the two Americas. In fact, it seems that we could even assume as more probable a migration from Africa to the southern part of North America than from these same southern parts to South America. Perhaps should it be wise to not absolutely ignore such an eventuality!

The comparative study by Durette-Desset (1971) of internal parasites of Caviomorpha and Phiomorpha has shown peculiar relationships between Heligmonellidae genera infesting Caviomorpha and one genus infesting *Thryonomys*, African recent Phiomorpha. Is that also only parallelism, superimposed to parallelism of the infested Rodents?

In conclusion, we think that the number and the weight of the arguments implies for the rodent a migration by rafts from Africa to South America between Middle Eocene and Oligocene.

Certainly the documentation about Primates is far less rich, even if some important arguments can already be proposed suggesting the same conclusion for their group. But it appears that the strength of these arguments is greatly reinforced when we know that Primates were already present in Oligocene Deseado, precisely at the same time as the rodents. At the same time, and same conditions, similar possibilities were at hand for the Primates and for the rodents. The rafts good for rodents were certainly good also for Primates. All the possibilities being the same, if the rodent went, and they went, there is no reason to doubt that the Primates also did, if it can be shown that they had to do so.

Incidentally, in the present state of knowledge, we do not see any fact supporting the hypothesis of a migration from South America to Africa.

This paper was written when I received the paper of Wood (1973) on Eocene rodents from Texas. The presence, in the southern part of North America of the hystricognathous genus *Prolapsus* is certainly very interesting, but I cannot find it so conclusive as Wood. Once more, I will argue that it is not logical to propose mere parallelism when there is a complete series of common characters (Africa) and direct relationships after the sole presence of the single character of hystricognathy (North America). It is true that Wood assumed that the basic plan of the teeth is the same as that of the Caviomorpha, while nevertheless admitting that they are too advanced to be ancestral to them. But, in my opinion, the peculiar relationships of the hypocône with the other tubercles, to speak only of that point, puts the genus far away from the basic plan of the Caviomorpha as well as of the Phiomorpha. So, I do not think I have anything to change in the conclusions of this paper, which could even be reinforced.

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La présence des Primates en Amérique du Sud dès l'Oligocène, en même temps que les Rongeurs et à côté d'eux, suggère une histoire similaire. Les ressemblances anatomiques entre les Rongeurs Africains. (Phiomorphes) et Sud Américains (Caviomorphes) ne peuvent s'expliquer de façon satisfaisante que par des relations de parenté directe. Dans la perspective de la Dérive des continents, on peut montrer que le passage par radeaux d'Afrique en Amérique, même s'il n'était pas aisé, était certainement possible pour les Rongeurs au début du Tertiaire, ce qui entraîne la même possibilité pour les Primates.

Robert Hoffstetter

Laboratoire de Paléontologie des
Vertébrés et Paléontologie Humaine,
Université de Paris VI,
4 Place Jussieu, F. 75005 Paris,
France

and

Institut de Paléontologie,
Mus. Nat. Hist. Nat.,
8, rue de Buffon, F. 75005 Paris,
France

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Phylogeny and Geographical Deployment of the Primates

A classification of the Primates into three suborders is adopted.

The *Paromyiiformes*, possibly derived from the Purgatorinae, illustrate an early radiation localized in time (Late Cretaceous—Eocene) and space (North America and Europe).

The *Strepsirhini* pose phylogenetic problems: position of the Daubentonidae; position of the Cheirogaleidae (possible Lorisidae); interrelations of the Adapoidea, Lemuroidea and Lorisidae. The cradle of the group was probably situated in Africa, which would have been the source of migrations towards Eurasia and Madagascar. It is not excluded that Madagascar could be the place of origin of the African Lorisidae.

The *Haplorhini* are divided into two sister-groups, early differentiated by geographical segregation on both sides of the Tethys. The Tarsiiformes, exclusively Laurasian, may have originated in North America, but their relationships with the Paromomyiiformes remain problematical. The Simiiformes (= Anthropeidea) have almost certainly originated in Africa. A transatlantic migration towards the end of the Eocene constitutes the most probable hypothesis (here put forward) to explain the colonization of the neotropical region by the Platyrrhini. The Catarrhini, at first exclusively African (the question of the fossils from the Eocene of Burma remains open) have invaded Eurasia since the Miocene (arrivals at intervals since the middle Miocene) thanks to the new geographical connections resulting from the Alpine orogeny.

1. Introduction

In spite of active—and often preferential—researches, our paleontological knowledge of the Primates remains fragmentary, and it is to be feared that many gaps will never be filled, for it is a group fundamentally linked to the tropical forest, an unfavourable environment for fossilization. Consequently, the origin, the phylogenetic relationships of the several branches, their distribution in time and space, pose many problems, and it might appear premature to attempt to trace biogeographical history.

Notable progress has been made, however, during recent years. An agreement has practically been reached as to the limits of the order, in spite of the problems posed by extinct forms. The most ancient fossils, and therefore the first radiations are already better known, principally in North America and in Europe too. By and by, we are leaving behind the confusion that has enveloped the history of the Hominoidea. Anatomical, caryological, biochemical, ecological and ethological studies are providing important data on the phyletic relationships between the surviving branches. Lastly, the mobilist conceptions of modern paleogeography enable us to reconsider the problems of migrations and settlement and suggest answers to questions which may have appeared insoluble.

Some attempts have recently been made, concerning the geographical dispersion of the Primates during geological times. Let us cite among others McKenna (1967), Hoffstetter (1971, 1972, 1973) and Walker (1972), the former in a fixist conception of paleogeography, the latter two adopting mobilist ideas. These are but working hypotheses, sometimes fragmentary ones. Perhaps the time has come to “faire le point” by trying to go closely into the known facts, and to explain them, according to the principle of parsimony of hypotheses. The future will tell us what we should keep, modify, or put aside.

2. Comprehension and Classification of Primates

Among extant Primates, zoologists and biochemists generally agree to recognize four natural groups, often considered as infraorders. These are the Lemuriformes, Lorisiformes, Tarsiiformes and Simiiformes (= Anthropoidea*). All post-Eocene fossils, and most of those from the Eocene can be assigned to one or the other of these taxa (in which, however, they represent some extinct families and superfamilies); therefore, it seems that the four extant groups have differentiated very early during the Tertiary (with the possible exception of the Lorisiformes, which are known since the Miocene only). The more ancient fossils, particularly those from the Paleocene, to which must be added their direct descendants in the Eocene, present, together with evidently primitive features, some unexpected specializations in such ancient forms; they represent an early radiation, and do not belong to the recent infraorders. They have been grouped in a special taxon, the infraorder Plesiadapiformes (Simons, 1973; Tattersall, 1972) or suborder Paromomyiformes (Szalay, 1973). In it is included, somewhat artificially, the genus *Purgatorius*, the only Primate to be known in the Late Cretaceous and early Paleocene, of which only isolated teeth have been collected so far, which does not allow us to ascertain whether it was already engaged in the evolutive trend followed by the undoubted Paromomyiformes.

Some other families, such as the Tupaiidae, Anagalidae, Apatemyidae, of which it had been supposed that they belonged to the Primates, are now excluded from them by the specialists. A doubt subsists for the Microsyopidae, about which opinions remain divergent.

The subordinal classification (i.e. the regrouping of some of the cited infraorders) has not yet met with a general agreement, but that seems to be approaching.

As for every group, the usual classification, at first essentially typological ("horizontal"), tends to approach a phylogenetical (or cladistic, or "vertical") classification, while our knowledge progresses, but this aim remains unattainable if we want to include all recent and fossil forms (see Hoffstetter, 1973).

According to this view, the Prosimii Illiger 1811 were first contrasted with the Simii = Anthropoidea (Simiiformes in the present work). This subdivision, still frequently used, is clearly "horizontal", since Van Valen, who adopts it (1969), precises that "the suborder Prosimiae is meant to include all Primates not sufficiently evolved to warrant a separate suborder".

All authors agree to recognize the group Lemuriformes + Lorisiformes as a natural unit (Walker even makes of it a simple superfamily, which may be a source of confusions), for which the name Strepsirhini Geoffroy 1812 has been proposed. In the same way, the

* I have proposed (Hoffstetter, 1974) the term Simiiformes to designate the infraorder which regroups monkeys, apes and men. Anthropoidea, generally used with the same meaning, has two drawbacks. It can be confused with "Anthropoides", currently used in various languages with the meaning of apes. On the other hand (recommendation 23 A of the Code of Nomenclature), the termination *oidea* must be reserved for superfamilies. As a matter of fact, the term Simii van der Hoeven 1833 or Simiae Haeckel would have priority (if the rule of priority was applied above the family group), but it literally means monkeys, which excludes the Hominidae. Simiiformes is constructed like the names of the other infraorders of Primates, and its use is justified by a precedent, since Tarsiiformes Gregory 1915 has been universally adopted to replace Tarsii Gadow 1898.

unit monkeys + apes + men, i.e. the Simiiformes, is practically recognized (though the natural character of this unit is denied, at least implicitly, by the supporters of an independent origin of the Platyrrhini and the Catarrhini; see further).

But the Tarsiiformes pose a problem. They have been included in one or other of both preceding groups. The presence of numerous primitive features, even in the recent forms, has caused them to be placed among the Prosimii ("horizontal" classification). However, the fact that they possess evolved characteristics, which they share with the Simiiformes (placentation, nostrils and teguments of the nasal region), and also their biogeographical history (Hoffstetter, 1972), and immunological studies (Goodman, 1972) justify their inclusion, together with monkeys, apes and men, in the suborder Haplorhini Pocock 1918. This conception is receiving more and more adhesions, but we must mention a very recent opposition (Gingerich, 1973), to which we shall come back later.

On the other hand, the Paromomyiformes (which have also been placed among the Prosimii), represent a particular radiation, apparently independent from that of the Strepsirhini. They must be considered as a suborder of their own, with the remark that the meaning of *Purgatorius*, and its relationships with the (unknown) stems of the other suborders are still problematical.

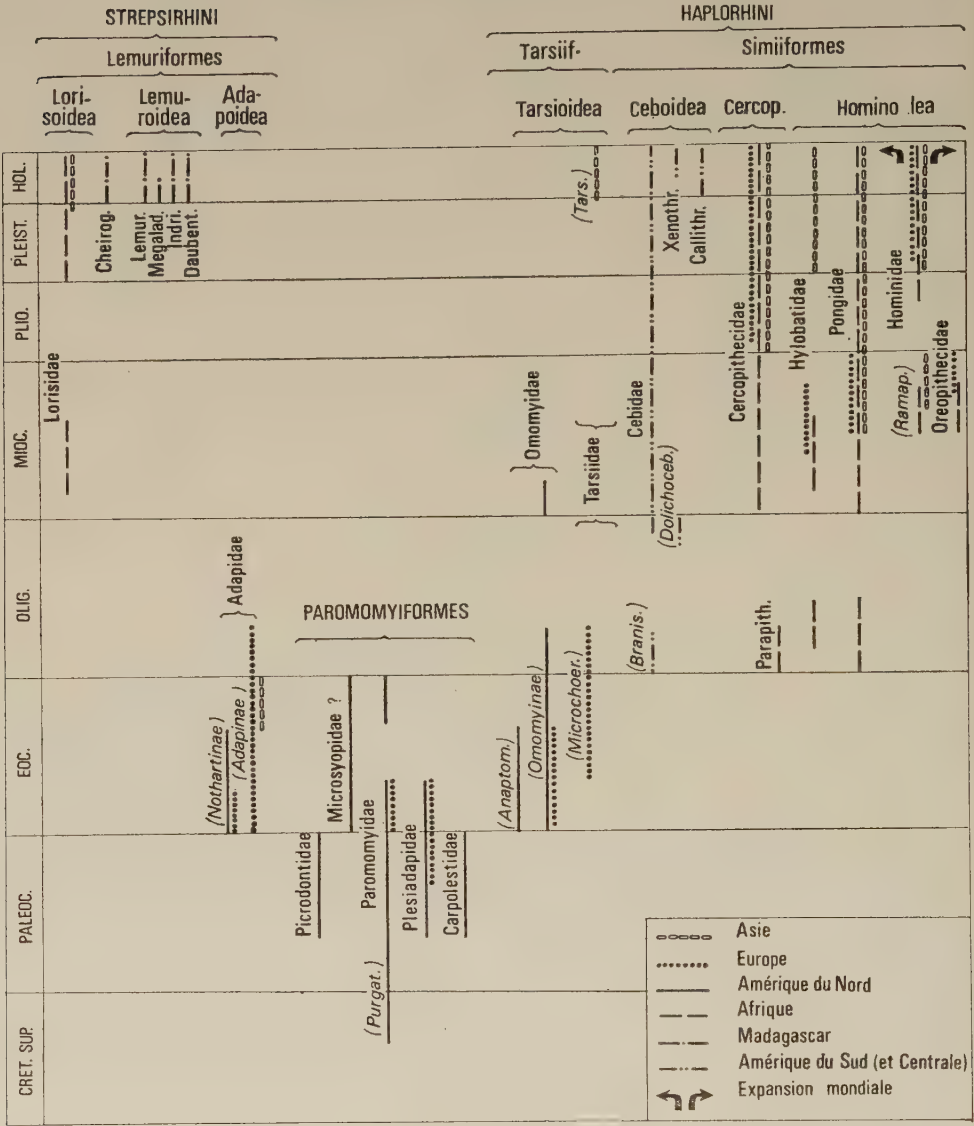
We shall adopt the following classification (see Figure 1 for distribution in space and time):

S.O. & I.O.	PAROMOMYIFORMES = PLESIADAPIFORMES	
	<i>Plesiadapoidea</i> :	Paromomyidae (incl. <i>Purgatorinae</i>); Microsyopidae?; Plesiadapidae; Carpolestidae; Picrodontidae.
S.O.	STREPSIRHINI	
	I.O.	LEMURIFORMES
		<i>Adapoidea</i> : Adapidae (incl. <i>Notharctinae</i>).
		<i>Lemuroidea</i> : Lemuridae*; Indriidae; Megaladapidae.
		(<i>Daubentonioidea</i> ?)**: Daubentoniidae.
	(I.O.	LORISIFORMES?)**
		<i>Lorisoidea</i> : Lorisidae; ? Cheirogaleidae*.
S.O.	HAPLORHINI	
	I.O.	TARSIIFORMES
		<i>Tarsioidea</i> : Tarsiidae (incl. <i>Microchoerinae</i>).
		(<i>Omomyoidea</i> ?)**: Omomyidae (incl. <i>Anaptomorphinae</i>).
	I.O.	SIMIIFORMES
		Platyrrhini
		<i>Ceboidea</i> : Cebidae; Xenothricidae; Callithricidae.
		Catarrhini
		<i>Cercopithecoidea</i> : Parapithecidae; Cercopithecidae.
		<i>Hominoidea</i> : Hylobatidae; Pongidae; Hominae; Oreopithecidae.

* The Cheirogaleinae, usually included in the Lemuridae, are here elevated to the rank of family and placed, with reserves, in the Lorisoidea (see further on).

** The infraorder Lorisiformes and the superfamilies Omomyoidea and Daubentonioidea may not be justified as taxa of such ranks.

Figure 1. Distribution of Primates in time and space. Inadvertently the presence of Omomyinae in the late Eocene of Asia (see text) is not represented in this diagram.



3. The Radiation of the Paromomyiformes—*Purgatorius* and the Origin of the Primates

The modern ideas on the comprehension of the Paromomyiformes and the phyletic relationships of their main branches appear clearly in Szalay's Figure 27 (1969), p. 317. However, some points remain debatable:

- (a) Inclusion of *Purgatorius* (Late Cretaceous–early Paleocene of North America) in the suborder, and its relationships with the Paromomyidae.

(b) Inclusion of the Microsyopidae (Eocene of North America) in the Paromomyiformes, and even in the Primates. Szalay has proposed (1969), then abandoned, it. Bown & Gingerich (1973) take it up again, arguing that *Microsyops* may be derived from the paromomyid *Plesiolestes*.

(c) Position of the Saxonellinae (*Saxonella*, from the late Paleocene of Germany) that Russell refers to the Carpolestidae, while Szalay, and Simons too, place them near the Plesiadapidae.

(d) Position of *Navajovius* (Colorado) and *Berruvius* (Cernay), both from the late Paleocene, first referred to the Tarsiiformes (Omomyoidea). Szalay (1969, 1973) places them among the Paromomyiformes, near the Microsyopidae, or among the Paramomyiidae (at least *Navajovius*), while admitting, however (1969), that relationships with the Omomyidae are possible. Simons does not take sides.

However that may be, this is a group which is known only in North America and in Europe. The undoubted forms appear in the middle Paleocene, *Purgatorius* as early as the Late Cretaceous. It seems that this is an instance of a localized radiation, characterized by a "rodent-like" specialization (convergence or real relationship with the rodents).

Everything leads us to believe that the group was born in North America; indeed, the five families here included (Paromomyidae, Microsyopidae, Plesiadapidae, Carpolestidae, Picrodontidae), and also the possibly ancestral Purgatorinae, are known there. On the other hand, Europe has harboured but two of these families (or 3, according to the place given to *Saxonella*), with 5 genera, 3 of which are also known in North America. The picture seems to be clear enough, despite the lack of evidence about the European faunas anterior to the late Paleocene.

This first radiation of the Primates may be added to other examples to demonstrate the existence of direct faunal exchanges between North America and Europe at the beginning of the Tertiary by North Atlantic route. At the same epoch (and up into the Oligocene) Europe was separated from Asia by an Ouralian sea. No direct exchange of Primates is demonstrated at that time between North America and Eastern Asia, though other groups (Notoungulata, Tapiroidea, Brontotheriidae, Pantodonta, Dinocerata, etc.) provide positive evidence. Perhaps the passage was forbidden to the Primates due to its latitude? Or perhaps the Asiatic Primates from the Late Cretaceous-middle Eocene period have so far escaped the researches (no systematic washings in the known localities)?

The inclusion of *Purgatorius* in the Paromomyiformes is defensible and probably legitimate, but not demonstrated since only isolated molars and premolars are yet known. The genus may be at the origin of the Paromomyiform radiation, but Szalay himself remains very careful, and places it on an offshoot (Purgatoriinae), issuing from the stem of the suborder.

But it would be rash to place *Purgatorius* at the origin of all Primates and to locate the cradle of the order in North America. Let us recall the scarcity of our knowledge of Late Cretaceous mammals, even on the continents where localities are already known. Let us also stress the sudden appearance, at the beginning of the Eocene, of two new groups of Primates in Laurasia. The one, Tarsiiformes, *might* be derived from the Paromomyiformes (problem of *Navajovius* and *Berruvius*). The other, Lemuriformes, seems to correspond to an immigration, perhaps originating in Africa; clearly, it has reached North America from Europe. We should therefore expect to discover, at its stem, forms related to *Purgatorius* (I postulate, until the contrary has been proven, a monophyletic

origin of the Primates), but distinct from it, the centre of radiation of which is evidently not North America. It would be fruitless, for the time being, to speculate on the place of origin of the common ancestor of Paromomyiformes, Strepsirhini and Haplorhini, but one cannot exclude Africa under the pretext that, contrary to Laurasia, it has not yet provided pre-Oligocene Primates.

The extreme position adopted by Walker (1972), who assumes *a priori* a world-wide extension (Madagascar and South America included) of an ancestral Primate stock, does not fit the already known facts.

4. The Strepsirhini and the Problems of Their Phylogeny

All authors agree to consider the Strepsirhini (Adapoidea, Lemuroidea, Lorisioidea) as a natural unit. However, the phyletic relationships between all three superfamilies, and even the comprehension of the latter two, pose serious problems. One of them concerns the Malagasy Daubentonidae, which are sometimes considered as a superfamily of their own; its specialization curiously recalls the Plesiadapidae, but it is practically certain that it is but a convergence towards a rodent-like type; on the other hand, the structure of the auditory bulla and its relationships with the ectotympanic suggest a common origin with both Adapoidea and Lemuroidea. Another moot point is the position of the Cheirogaleinae, usually included in the Malagasy Lemuridae, with the rank of a subfamily; now, some of their features had led the old authors (Flower and Lydekker as early as 1891, and Forbes in 1895) to see in them transitional forms between Lemuroidea and Lorisioidea (which is confirmed by the modern studies of Charles-Dominique, Martin and Szalay); we shall consider them here as a family of their own (Cheirogaleidae), the inclusion of which in the Lorisioidea or the Lemuroidea must be discussed. We shall also see that the probable phylogenetic relationships of the constituent branches of the Strepsirhini lead us to consider the classical division into Lemuriformes and Lorisiformes unsubstantiated. To make it clear, we shall consider separately three superfamilies (Adapoidea, Lemuroidea, Lorisioidea) and two aberrant taxa (Daubentonidae and Cheirogaleidae) inside the suborder.

The difficulty lies in the scarcity of the paleontological data, since we only know disjointed units, both in time and space: Adapoidea in the Eocene and the early Oligocene of Laurasia; Lorisioidea from the Miocene to the Present in Africa (see Walker, 1972*b*) and from the Pleistocene to the Present in Asia; Lemuroidea, Cheirogaleidae and Daubentonidae in the Holocene and the Present of Madagascar. Many hypotheses can be expressed to connect together those three groups, without it being possible to choose with any certainty.

Before we tackle the biogeographical problem, it is necessary to discuss the main possible phylogenies.

From an anatomical point of view, four apomorph (= derived) characters enable us to classify the known Strepsirhini:

(a) Extension of the bulla beyond the tympanic ring, which gets included (so-called lemuroid disposition); I am convinced, with Szalay (1972) and contrary to Gingerich (1973), that it is a derived condition, as compared with that in primitive mammals and also in Paromomyiformes and Haplorhini (see Hoffstetter, 1974).

(b) So-called lorisoid pattern of carotid circulation, recently restudied and discussed

by Szalay & Katz (1973); it is essentially characterized by the acquisition *de novo* of an anterior carotid artery and by the atrophy, ending in its disappearance, of the stapedia artery.

(c) Differentiation of a lower dental "comb", including the incisors and the canines, while the P_2 becomes canine-like.

(d) "Rodent-like" specialization of the dentition and the lower jaw.

The distribution of those characters among the Strepsirhini is as follows:

	Adapoidea	Lemuroidea	Lorisoidea	Cheirogaleidae	Daubentoniidae
(a)	+	+	—	+	+
(b)	—	—	+	+	—
(c)	—	+	+	+	—
(d)	—	—	—	—	+

These associations of apomorph features seem to be contradictory from a phylogenetic point of view, and cannot be explained without assuming the existence of convergences (independent acquisition of the same apomorph character in several lineages) or of regressive evolutions (return to the plesiomorph or ancestral disposition).

Now, convergences are all the less probable as the character is more complex. In particular, the repeated appearance of character (b) is highly unlikely (see Szalay & Katz, 1973). Even the dental comb (c) runs few chances to get realized under an identical shape in several branches. A convergence bearing upon feature (a), though not very probable, seems to be less unlikely since it only involves an extension of the bulla beyond the tympanic ring; let us note, by the way, that the same disposition has been acquired independently outside the Primates, in the Tupaiidae (and also in the Leptictidae: see McKenna, 1963, 1966), from a bulla constituted by the entotympanic, not the petrosal; this ascertained convergence from different skeletal elements, makes *a fortiori* more likely a parallel acquisition of the same structure from the same bony material; nevertheless, it remains strange that this lemuroid bulla is found in all Malagasy Primates and in all the Strepsirhini known before the Miocene.

A regressive evolution also seems to be impossible for character (b), which entails notably the atrophy of the stapedia artery. It is less unlikely for character (a): a derivation of the lorisoide disposition (ring outside the bulla as in primitive Mammals) from that of the *adult* Lemuroidea is evidently unthinkable; but the latter present ontogenic stages which are practically identical with those of the Lorisoidea (see Van Kampen 1905, Figure 91, p. 678); thus a simple blocking of the development of the bulla during ontogenesis would be sufficient to come back to the ancestral condition.

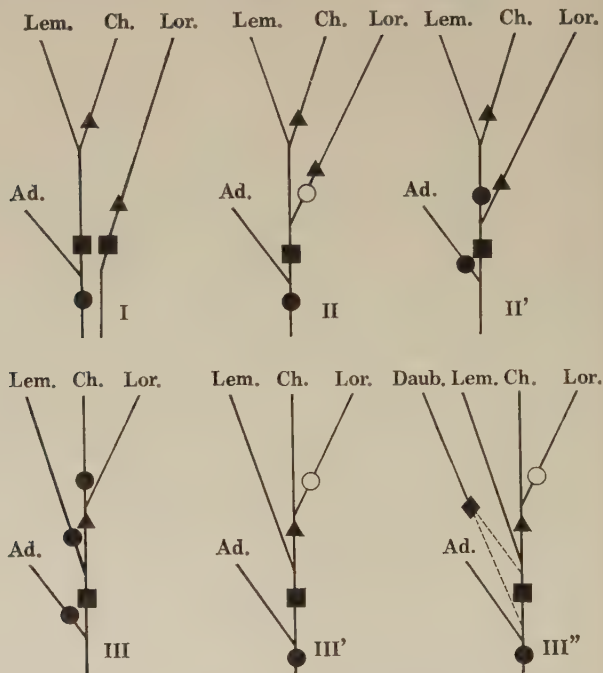
The problem posed by the Daubentoniidae is real but will be easily solved as soon as some fossils are known. This is the only family of the Strepsirhini which shows a rodent-like specialization; that can be derived from an "adapoid" stage (without a dental comb) or from a lemuroid stage (with a dental comb). The number of archaic features (primitive brain, claws, and so on) retained by the Aye-Aye, however, would rather lead to assume an early separation, soon after the acquisition of the lemuroid bulla.

Leaving aside that aberrant family for the time being, we can consider several phylogenies linking together the other Strepsirhini. Three main ones will be distinguished (Figure 2) according to whether we shall consider as more unlikely the repeated appearance of apomorph characters (a), (b) or (c).

Diagram I (Figure 2) corresponds to the classical conception, in which the initial dichotomy (Lemuriformes/Lorisiformes) is marked by the acquisition of the lemuroid bulla (a) by the former. It is clear that this requires at least two convergences, both very unlikely, concerning features (c) and (b).

Diagram II (Figure 2), more in conformity with the ideas of many modern authors, considers a common trunk for Lemuroidea and Lorisioidea (acquisition of the dental comb), while the Adapoidea would have separated earlier. Two variants are offered

Figure 2. Hypotheses about the phylogeny of the Strepsirhini: (a) ●, acquisition of lemuriform disposition of the bulla and the ectotympanic; ○, loss of the same character; (b) ▲, acquisition of lorisoid pattern of carotidian circulation; (c) ■, acquisition of lower dental comb; (d) ◆, acquisition of rodent-like dentition of the Daubentonidae.



(Figure 2, II and II'), according to whether we consider as more likely the early acquisition of the lemuroid bulla (a) and then its loss by the Lorisidae (II), or the independent acquisition of this same bulla by the Adapoidea and the Lemuroidea + Cheirogaleidae (II'). In both eventualities, the independent acquisition of the lorisoid pattern of carotid circulation (b) by the Lorisidae and the Cheirogaleidae, which seems to be highly unlikely, we stress it again, must be assumed.

To answer this objection, and also to explain ethological and ecological observations (Charles-Dominique & Martin, 1970), one is led to bring together the Cheirogaleidae and the Lorisidae (diagrams III and III', Figure 2), both groups having inherited character (b) from a common ancestor. Both variants concern character (a), which can appear three times (Figure 2, III), or only once with return to the ancestral disposition in the Lorisidae (Figure 2, III'). According to the principle of parsimony of hypotheses, and taking into account the preceding remarks, the last diagram (III') seems to us, at least in the present state of our knowledge, the most likely.

At this stage we can try to place the Daubentoniidae in the same diagram (Figure 2, III"), rooting them in before or after the acquisition of the dental comb. Let us recollect that the primitive features of the modern form render more likely an early rooting, without it being possible to be more precise.

The adoption of this phylogeny renders unreceivable the usual classification of the Strepsirhini. To respect at best the phylogenetic relationships of diagrams III' and III" (if they are accepted), it would be reasonable to recognize but one infraorder (Lemuriformes *s.l.*) in the Strepsirhini, and to distinguish inside it three or four superfamilies: Adapoidea, Lemuroidea, Daubentonioidae(?) and Lorisoidae (including Cheirogaleidae).

The preceding line of reasoning, and therefore the choice between the hypotheses, rests essentially upon the interpretation of the anterior carotid artery that has been adopted by Szalay & Katz (and by Saban). But it cannot be excluded that this artery could be homologous to the mesial entocarotid of the primitive mammals. If that was the case, its persistence in the Cheirogaleidae and the Lorisidae would be a symplesiomorphy, which would by no means be proof of a close kinship. One could then come back to a scheme alike to those which Hill (1953, t. I, p. 28) and Martin (1972, p. 301) have proposed, with, however, some corrections about the position of the Adapidae. Nevertheless, the arguments put forward by Szalay & Katz are rather convincing, and, above all, the ethological observations of Charles-Dominique & Martin also reveal some apomorphic characters which are shared by Cheirogaleidae and Lorisidae.

An important contribution could be provided to this problem by biochemical and immunological studies. For the time being, the results are somewhat contradictory (compare the diagrams provided by Goodman and McLaughlin, among others). To the extent of my knowledge, Cheirogaleidae and Galaginae unfortunately have not been subjected as yet to such researches.

Other evidence (difficult to interpret from a phylogenetic view point) can be found in modern biometrical studies. In this way, according to Lessertisseur, Nakache & Petit-Maire (1974), the study of the cranio-facial features (16 parameters) with the help of the factorial analysis of correspondences, has shown that the Cheirogaleinae are (typologically) far removed from the Lemuridae (but near the Indriidae!); their own cloud is situated in the vicinity of the Lorisidae, more precisely near the larger Galaginae for *Cheirogaleus* and the smaller Galaginae for *Microcebus*.

The previous considerations, of a phylogenetic order, allow us to consider the problem of the geographical spreading of the group, without clearing it up completely, however.

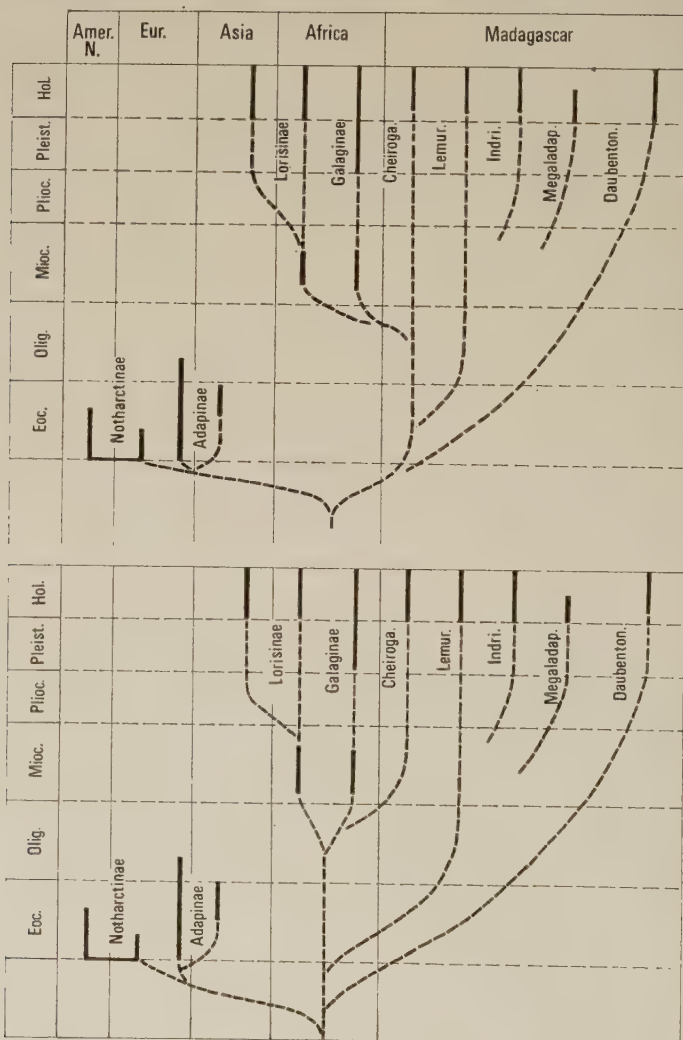
The earliest known Strepsirhini (Adapoidea) are Laurasian. But they appear suddenly in the early Eocene (Europe and North America), and we do not know local ancestors. It is impossible to have them derived from the Paromomyiformes, which are too specialized. Even a descent from *Purgatorius* remains very problematical, for geographical reasons, because the North American Adapidae (Notharctinae, characterized by their molars bearing a pseudohypocone) are clearly immigrants and constitute a derived group, by comparison with the Eurasian Adapinae. The cradle of the group is probably not Europe (no stem form known in the Cernaysian fauna). It could be situated in Asia, where the adequate localities have not yet been subjected to methodical washings. It corresponds more probably to Africa, which unfortunately has not yet provided any small mammal from the Cretaceous-Eocene period.

Anyway, an ancient African strepsirhinian stock (sister-group of the Adapoidea? or

ancestral group?) is necessary to explain the settlement of Madagascar. It is undoubtedly at the beginning of the Tertiary (Eocene ?) that this island received the founders of its Primate fauna, which have had to cross a sea barrier. According to our present paleogeographical knowledge, Africa almost certainly is the place of origin of those immigrants. India is much more unlikely, be it only because it is impossible to imagine whence and how it could have received its own Primate fauna while it was isolated in the Indian Ocean!

The lack of Tertiary Malagasy fossils, and of African pre-Miocene Strepsirhini too, prevents us from knowing the number and the time of the Primate settlements in Madagascar. To put it as simply as possible, one colonization, which would be the origin of a Malagasy radiation ending in the Lemuroidea (Lemuridae, Indriidae, Megaladapidae),

Figure 3. Two hypotheses about the geographical distribution of the Strepsirhini, the phylogeny of diagram III' (Figure 2) being admitted. Ad. = Adapoidea; Ch. = Cheirogaleidae; Daub. = Daubentoniidae; Lem. = Lemuroidea; Lor = Lorisidae.



the Daubentoniidae, and the Cheirogaleidae, would be sufficient; from the earliest representatives of the latter, according to the adopted phylogeny (Figure 3, upper part), a migration, of Malagasy origin, would be the stem of the African Lorisidae, early differentiated into Galaginae and Lorisinae; the Asian settlement by the Lorisinae perhaps would be later than it has been believed to be, since, according to Tattersall (1969), *Indraloris* (Miocene of India) is not a lorisid.

But one may also imagine that the differentiation of the Malagasy groups has taken place in Africa (Figure 3, lower part), with an early migration of the Daubentoniidae and the Lemuroidea towards Madagascar. The African stems would have disappeared locally, after having given rise to the Lorisioidea, an early branch of which would have reached Madagascar (third migration), to produce there the Cheirogaleidae.

These are but two variants, both conjectural, founded upon the same phylogenetic interpretation. The first one would account in a simpler way of the known facts (lack, at least apparent, of Strepsirhini in the African Oligocene), but the Malagasy origin of the Lorisioidea runs the risk of encountering widespread reluctance! In the second hypothesis, one may surmise that the African Lemuroidea have disappeared early enough and that their lorisoid successors were restricted during the Oligocene in the Eastern and Central African forest.

All of this presupposes the existence of Strepsirhini in Africa at the beginning of the Tertiary, as McKenna had already assumed (1967). This existence is compelling to explain the phylogenetic relationships between Adapoidea and Lemuroidea, and also between Lorisidae and Cheirogaleidae. We cannot follow Simons (1972), who doubts it, because, he writes, such a presence would have had as a consequence a greater diversity of the subsequent forms of African Primates. We have already answered this objection by assuming the early extinction of the African lemuroids (perhaps brought about by the monkeys, for it is to be remarked that the coexistence of both groups in the same place has never been observed) and the localization of possible Oligocene lorisoids in Central and Eastern Africa.

Of course we consider as gratuitous Walker's hypothesis (1972), according to which "lemuroids" (taken in the meaning of Strepsirhini) would have inhabited South America from the late Paleocene to the early Eocene (!)

5. The Haplorhini and Their Dichotomy

Because of the evidently primitive features retained by their present day representative (*Tarsius*), the Tarsiiformes have long been placed in the suborder Prosimii, as opposed to the Simii = Anthropoidea (i.e. Simiiformes).

Hubrecht was the first, as early as the end of the XIXth century, to observe that the placenta of *Tarsius* (discoidal, deciduous) separated the latter from the lemurs, loris, and galagos (= Strepsirhini, with a diffuse, aedeiduous placenta), and to bring it near the Simiiformes.

Moreover, Pocock (1918) has shown that the Strepsirhini possess a rhinarium with a naked and moist skin, which reaches the upper lip, and nostrils with a split edge (primitive features inherited from the "Insectivora"); on the contrary the nose of *Tarsius*, with a hairy, undifferentiated skin and rounded nostrils with entire margins (derived = apomorph characters) fits in with that of monkeys, apes and men. Consequently, he has regrouped the Pithecoidea (= Anthropoidea) and the Tarsioidea into a "grade" of the

Haplorhini, as opposed to the "grade" of the Strepsirhini (curiously, Pocock uses the term "grade" in an unusual meaning, while his proposition is a first approach towards a cladistic classification!).

This proposition received but few adhesion, and almost all authors have continued to divide the Primates into Prosimii and Anthropoidea: let us cite Simpson, Vallois, Piveteau and recently McKenna (1967), Van Valen (1969), Simons (1972), to name but some of the most prestigious. Hill (1955) alone has adopted Pocock's classification.

As soon as 1970 (published 1972), chorological consideration have led me to consider Tarsiiformes and Simiiformes as two sister-groups, which have differentiated by geographical segregation on each side of the Tethys. Anatomical and biochemical evidence has been added to Hubrecht's and Pocock's observations to confirm this view. Thus, Luckett (1972) by widening and deepening the studies about the placenta and the foetal annexes, has shown that *Tarsius* differs from the Strepsirhini and fits in with the Simiiformes by its chorio-allantoic placenta, which is discoidal and hemochorial, by the reduction of the allantoic vesicle and the yolk sac, and at last by the absence of a chorio-vitelline placenta. On the other hand, Goodman (1972), on an immunological basis, has pointed out that "In the early Primates, four major lines branch apart, separating the ancestors of lemuroids, lorisooids, *Tarsius* and Anthropoidea, with the lorisooids and lemuroids sharing a slightly more recent common ancestor with each other, and, similarly, *Tarsius* and Anthropoidea sharing a slightly more recent common ancestor before branching apart". Moreover, Goodman, Barnabas & Moore (1972: 671), stress the fact that "the observations by Barnicot and Ewett-Emett (1972) on an A₂-like hemoglobin in tarsier but not in lorisooids or lemuroids suggest that an original beta-proto delta duplication had occurred in a primitive tarsioid-like line ancestral to *Tarsius* and Anthropoidea".

It is satisfying to note that those arguments have already convinced a number of students of the fact that the division of the Primates into Strepsirhini and Haplorhini and the early dichotomy of the latter, ending in the Tarsiiformes and the Simiiformes, are well founded.

However, Gingerich (1973) adopts a quite contrary position. Having observed, on a fragment of a squamosal of *Apidium* (a monkey from the early Oligocene of Africa), an indication of a fusing of the posterior crus of the ectotympanic, but only a simple area of contact for the anterior crus, he concludes that the bulla and the ectotympanic of *Apidium* (which have not been preserved) must have shown the lemuroid disposition. According to him, this condition would be phylogenetically primitive in the Primates, and he infers from it that the Anthropoidea (= Simiiformes) would be descended from a lemuroid ancestor, possibly a species of *Pelycodus* (a notharctine from the early Eocene of North America and Europe), without passing through a tarsioid stage.

Those points call forth serious reserves (Hoffstetter, 1974). Let us note, firstly, that it is very doubtful whether the lemuroid structure is primitive in the Primates. The presence of the same disposition in the Tupaiidae, mentioned by Gingerich in support of this thesis, clearly is a convergence, since the bulla is of a different nature; therefore the argument turns back against the primitive character of such a condition. Moreover, to follow Gingerich, it would be necessary to admit that this "primitive" structure has later been lost independently (return to the ancestral mammalian disposition with the ectotympanic outside the bulla) by the Plesiadapiformes, the Lorisidae, the Tarsiiformes, and the

Simiiformes (several times in the latter if, with Gingerich, we suppose a separate origin of Platyrrhini and Catarrhini from the Lemuriformes).

It will also be noted that the derivation of the Simiiformes (molars with a true hypocone) from the Notharctinae (molars with a pseudohypocone) would need a solid demonstration.

As a matter of fact, there is a flagrant disproportion between Gingerich's observations and the conclusions he draws out of them. As he himself says, the absence of fusing of the anterior crus of the ectotympanic with the squamosal "suggests" a lemuroid condition in *Apidium*; it does not demonstrate it. In all other known Simiiformes, including *Aegyptopithecus*, from the same locality and level as *Apidium*, the ectotympanic remains outside the bulla. If then Gingerich's interpretation turned out to be exact (of which I am strongly in doubt, for his figuration of the petrosal is almost identical with that of a platyrrhinian), perhaps it would be convenient to consider *Apidium* as an aberrant offshoot, rather than to question the whole phylogeny of the Primates, and to have recourse to multiple convergences to explain the presence of common apomorph characters noted in the Tarsiiformes and the Simiiformes.

6. The Tarsiiformes, A Laurasian Group

In the dichotomy the Haplorhini have gone through, the Tarsiiformes represent the pleisiomorph group: indeed, even their modern representative retains a number of archaic features (smooth brain, primitive tooth pattern, bifid uterus, . . .), associated, it is true, with already cited apomorph characters, which are also present in the Simiiformes (therefore diagnostic of the Haplorhini), and also specializations of its own, which are not general in the infraorder. However, it will be noted that the development of an external auditory tube as early as the Eocene in *Necrolemur* (while this tube appears but later in the Catarrhini and never in the Platyrrhini) speaks in support of an early separation of Tarsiiformes and Simiiformes. That is why I consider them as two sister-groups, and not as two successive groups, the one derived from the other.

Tarsiiformes are known only in Laurasia. They appear suddenly in the early Eocene in North America and in Europe, but they are ascertained only a little later (late Eocene?) in Eastern Asia.

The family Omomyidae (which is sometimes considered as a superfamily of its own), widely distributed during the Eocene, later possesses only a few representatives, all of them North American. Two subfamilies (families according to some authors) are distinguished inside it. The Omomyinae have diversified mostly in North America, where 11 genera, all of them endemic, 9 of which from the Eocene, are known; two only are known in the early Oligocene (*Macrotarsius* and *Rooneyia*), and one only in the early Miocene (*Ekgmowechashala*). The European forms consist only of two genera, *Teilhardina* (early Eocene) and *Periconodon* (middle Eocene). Lastly, two poorly known genera from Eastern Asia, *Hoanghoni* and *Lushius* (late Eocene), are probably to be included in the same group. The other subfamily, Anaptomorphinae, exclusively North American, seems to be derived from the former, and comprises 8 genera, limited to the early and middle Eocene.

The Tarsiidae, somewhat later and probably issued from primitive Omomyidae, are exclusively Eurasian. Two subfamilies are also distinguished among them. The Microchoerinae are known but in Europe, and only during the middle Eocene-early Oligocene period. They comprise 4 genera, of which *Pseudoloris* alone crosses the Eocene-Oligocene boundary, without nevertheless going beyond Stehlin's "Great Cut". The Tarsiinae are

represented only by the modern genus *Tarsius*, restricted to the islands of South-Eastern Asia (Sumatra, Celebes, Borneo and the Philippines).

This paleontological evidence shows obvious gaps, so that the biogeographical history of the group is not clear. The distribution of the fossils and their assumed phylogenetic relationships suggest a North American cradle. On that continent the Omomyinae have known their major radiation, and there they have survived the longest. There they have given birth to a local subfamily, the Anaptomorphinae. The European Omomyinae could be but still little differentiated emigrants (*Teilhardina* is very near *Loveina*). But is it true that Asia is far from having given up all its secrets. However that may be, if we consider a North American origin, we can wonder from which stem? It is not to be excluded that it may be found among the Paromomyiformes, near such forms as *Navajovius* (North America) or its possible European relative, *Berruvius*, both from the late Paleocene. Both these genera, which are accepted as Primates by all authorities, have first been included in the Tarsiiformes, of which they would then be earliest representatives. But Szalay (1969) has expressed reserves about this inclusion, while recognizing, it is true (*ibid.*, p. 277) that "it is possible, however, that both *Navajovius* and *Berruvius* have close ties with the primitive omomyids". Simons (1972) recognizes them as Primates, but he does not insert them in his classification of the order. If no rooting of the Tarsiiformes turns out to be possible in North America, then it would be necessary to consider them as immigrants, perhaps from the West (?) that is, from Eastern Asia, since their expansion seems to have taken place from North America towards Europe. We still have no basis to build such a hypothesis upon.

The Microchoerinae, which have suddenly appeared in Europe during the middle Eocene, could be derived from local Omomyinae of the early Eocene, *Teilhardina* having already been suggested as a possible ancestor.

Lastly, the Tarsiinae, still unknown as fossils, can be descended only from (unknown) ancestors in continental Asia, themselves related to the preceding, though it is impossible to consider a direct descent from known Microchoerinae.

Walker (1972), moreover, postulates a southern expansion of the omomyids during the Paleogene. More precisely, he figures them in his scheme (p. 213), in South America and in Africa, from the late Paleocene until the early Oligocene, and he considers (text p. 214) their possible presence in Madagascar towards the Paleocene-Eocene boundary. That hypothesis is purely gratuitous as far as Madagascar is concerned. It is more justifiable for Africa, where the earliest ancestral forms of monkeys were perhaps, *typologically*, omomyoids (it will be suitable, when they are known, to look for some early differential character that would enable to classify them among the Simiiformes); however, it is known that, contrary to Walker's scheme, monkeys, not omomyids, are present in the Fayum fauna (early Oligocene), and their evolutionary stage leads to assume that they had differentiated in Africa far earlier. As far as South America is concerned, Primates appear there as immigrants having arrived towards the end of the Eocene (ascertained as early as the early Oligocene), having probably already reached the simian "grade" (see further).

7. The Simiiformes: Conquest of the World from Africa

Among all the Primates, the Simiiformes represent the infraorder which has met with the greatest success. It includes today 3 superfamilies, 6 families, and 35 genera. The

monkeys occupy almost the whole intertropical zone (with the exception of Madagascar and the Australo-Papuan region), and they extend widely outside it: in Eastern Asia, they are found today beyond 40° North latitude; and extinct forms have even reached beyond the 50th parallel both northward (Eurasia) and southward (South America). Some of them have succeeded in leaving the forest to live in the savanna, and even in semi-desert environment. Lastly, Man represents the unique case of a species which, not content with having conquered the whole world, has already achieved some extra-terrestrial explorations!

The unity of the group has been more or less explicitly doubted. For paleogeographical reasons (which are out of date today), one has been led to look for an independent origin for the New World monkeys (Platyrrhini) and those of the Old World (Catarrhini), from a Laurasian prosimian stem (more precisely an omomyoid one . . . unless, with Gingerich, we want to consider lemuriform ancestors!). In other words, the Simiiformes were considered as a diphyletic group, the unity of which was no longer acceptable from a phylogenetic point of view. Alone among the classifiers, Romer (1966) has drawn the logical conclusion by dropping the taxon "Anthropoidea" (= Simiiformes), and by dividing the Primates directly into five suborders, among which the Platyrrhini and the Catarrhini. Recent studies (see further) show that the arguments that have been put forward, of paleogeographical, anatomical and paleontological order, by no means compel us to accept this diphily; on the contrary, an origin of the Platyrrhini from African monkeys turns out to be much more likely, which leads to revalidate the taxon Simiiformes, including all monkeys, apes and men.

Origin of the Simiiformes

Before the Miocene, no simiiform is known North of the Tethys (we shall consider later the problem posed by two fossils from the burmese Eocene). This absence, in the whole of Laurasia, seems to be significant, because this is the supercontinent on which paleontological researches have been most intensive. If we take into account the fact that, from their anatomy and their biochemistry, the Tarsiiformes are the taxon phylogenetically nearest (I disregard here Gingerich's divergent opinion), and that they are exclusively Laurasian, we are led to assume that both infraorders are sister-groups, differentiated by geographical segregation on each side of the Tethys during the Paleogene. Only later, thanks to geographical changes, could the Simiiformes reach the northern continents, while the last survivor of the Tarsiiformes was taking refuge in the islands of South-Eastern Asia. It is therefore in the southern lands that we have to look for the origin of the Simiiformes. Unfortunately they are not ascertained until the early Oligocene. They appear suddenly in Africa (Fayum), with two superfamilies and three families (Parapithecidae, Pongidae and Hylobatidae), and in South America (Bolivia), with the one genus *Branisella*.

No local stem is known in South America, though adequate localities are known there (see further). So that the platyrrhinian monkeys (as well as the caviomorph rodents) have been recognized since long ago as immigrants, arrived in South America across marine barriers, at the beginning of the Oligocene or somewhat earlier.

On the other hand, the earliest African monkeys appear from the beginning as very diversified. They are certainly descended from local ancestors which remain to be discovered, for no African locality is known, which would have yielded small terrestrial

mammals from the Cretaceous–Paleocene–Eocene period. Let us recall that the few late Eocene localities show a very peculiar facies, in which the only mammals are cetaceans, sirenians and proboscideans. It is also to be noted that the only Oligocene monkeys collected in Africa are from the Fayum, but that the African fauna must have been far richer and more varied at that epoch, since we still do not know anything of the forms then living in Central and Eastern Africa, i.e. in the regions most suited to shelter Primates.

Accordingly, it is most probably in Africa that the cradle of the Simiiformes was situated. But, because of the lack of pre-Oligocene fossils, we remain in complete ignorance of the first phases of their history. In the same way, it is impossible, for the time being, to decide whether the common stem of the Haplorhini was austral (Africa) or northern (North America? Asia?). Unless it can be demonstrated that the Tarsiiformes were really born in North America from local Paromomyiformes. In such an event, it would be necessary to postulate that an early branch of the omomyoids would have reached Africa (through Europe or through Asia?), there to give rise to the Simiiformes.

Let us recall here, without considering it again, Gingerich's hypothesis (1973), who postulates a derivation of the Simiiformes from the Notharctinae: the type of the molars of the latter suffices to exclude them from the ancestry of the monkeys.

The fossils from the burmese Eocene

One cannot discuss the origin of the Simiiformes without touching upon the problem posed by two fossils from the late Eocene of Burma (Pondaung sands). Two genera (*Ponndaugia* Pilgrim 1927 and *Amphipithecus* Colbert 1937) have been described there. Among the various authors who have studied them or commented on them (Pilgrim, Colbert, Piveteau, Hürzeler, von Koenigswald, Szalay, Simons), Hürzeler has considered them to be unclassifiable, the others have referred them, always with reservations, to the Simiiformes, the Lemuriformes, or the Condylarthra. It shows that the pieces so far known do not warrant a sure interpretation. Even the latter hypothesis cannot be definitely rejected, at least on the basis of some arguments brought forth by Simons (1971): on the one hand, the lack of a diastema does not allow one to exclude them from the Condylarthra; on the other hand, representatives of the latter order are known in the Eocene of Asia, in Eastern Asia (Paleocene and Eocene) as well as South of the Himalayas (middle Eocene of Ganda Kas). Nevertheless, some other arguments seem to support the hypothesis according to which *Amphipithecus* belongs to the Primates (admitted by Colbert, von Koenigswald, Szalay and Simons), but it remains difficult, anyway, to precise its subordinal position. It should be noted, lastly, that it would be useful to know whether, during the Eocene, the Burmese locality was situated North or South of the Tethys (dates and hypotheses concerning the paleogeography of South-Eastern Asia are still very contradictory!). If it is true, as is stressed by Simons, that the Anthracotheriidae from the Pondaung locality may suggest faunal exchanges with Africa, on the other hand, the Brontotheriidae and the Tapiroidea speak for a communication with North America through Eastern Asia!

Origin and expansion of the Catarrhini

Though still far from complete, our documentation about the Catarrhini shows us that all the six families of the group are or have been present in Africa and have almost certainly

originated there. One is peculiar to this continent: Parapithecidae, localized in the early Oligocene. The five others have their earliest known representatives there: *Aegyptopithecus* and *Oligopithecus*, from the early Oligocene, for the Pongidae; *Aeolopithecus*, from the Oligocene, for the Hylobatidae; *Victoriapithecus* and *Prohylobates*, from the Miocene, for the Cercopithecidae; *Mabokopithecus* and ? *Oreopithecus*, from the Miocene, for the Oreopithecidae; *Ramapithecus*, from the Miocene, for the Hominidae (or *Australopithecus*, from the Plio-Pleistocene, if one refuses to include the former genus in that family).

This confirms the hypothesis of an African origin of the Simiiformes, or at least of the Catarrhini.

From a phylogenetic point of view, some problems still remain: relationships of the Parapithecidae and the Oreopithecidae with the other families; position of *Apidium*, taking into account Gingerich's observations (1973); antiquity and insertion of the Hominidae on the phyletic tree of the group. We shall not consider them here.

It is probable that, a little before the Oligocene, some African Simiiformes may have settled in South America, across the Atlantic Ocean; we shall consider this problem later. On the other hand, faunal exchanges with the Indian plate may have taken place, since, according to Lavocat, ancestral Phiomorpha (not yet described) have been discovered in the middle Eocene of Pakistan, consequently south of the Himalayas and before the Alpine orogeny.

From the Miocene onward, a terrestrial communication is reestablished, at least intermittently, between Africa and Eurasia, with, as a result, a massive faunal exchange, in which the Catarrhini are implicated. Their expansion, however, seems to have been delayed by comparison with that of other groups, but it spreads itself widely in Eurasia, as far westwards as Spain, and as far eastwards as Indonesia and Japan; but their climatic requirements have not allowed the monkeys to use the Behring "bridge", nor, consequently, to invade North America from Asia.

The Hylobatidae first appear in Europe with *Pliopithecus* (middle and late Miocene), but they are not ascertained in Asia until the Pleistocene. The Pongidae arrive soon after, with *Dryopithecus* (late Miocene of Europe and Asia), which is followed by the Asian genera *Gigantopithecus* and *Pongo*. The hominid *Ramapithecus* also reaches Asia during the late Miocene.

Curiously, the Cercopithecidae are later arrivals and are unknown in Eurasia before the Pliocene. The Oreopithecidae have made but a limited incursion, both in time and space, at the late Miocene of Tuscany, where they may have arrived directly from Africa, thanks to island stepping-stones across the Mediterranean. (However, it is to be noted that Simons (1972, p. 189) mentions their presence in Southern Russia, a fact which I have not been able to confirm.)

Origin and expansion of the Platyrrhini (= Ceboidea)

The neotropical monkeys constitute a superfamily (Ceboidea) which includes two families, Cebidae with 11 genera and Callithricidae with 2 genera. They inhabit the tropical forests, between the 25th N and the 30th S parallels. They are often called Platyrrhini, because of the width of their internarial septum, but this feature suffers exceptions (*Aotus*, *Alouatta*, *Brachyteles*). As far as the skeleton is concerned, they are distinguished

from the *modern* Catarrhini by the retention of some primitive features: 3 premolars (instead of 2); auditory bulla rather swollen; ring-like ectotympanic, not stretched into an ossified external auditory tube; orbito-temporal fenestra relatively large.

Fossils are few. With the exception of some representatives, little or not distinct from the modern ones (Quaternary of Brazil), they comprise but 7 extinct genera, from the Deseadian = early Oligocene of Bolivia (*Branisella* Hoffstetter 1969), the Colhuehuapian = latest Oligocene of Patagonia (*Dolichocebus* J. L. Kraglievich 1951), the Santacruzian = early Miocene of Patagonia (*Homunculus* Ameghino 1891), the late Miocene of Colombia (*Cebupithecia* Stirton 1951, *Neosaimiri* Stirton 1951, *Stirtonia* Hershkovitz 1970), and the Subrecent of Jamaica (*Xenothrix* Williams & Koopman 1952). These data demonstrate the temporary extension of the group down to 50° S latitude, and also the settlement of at least one of the Greater West Indies. On the other hand, no fossil monkey has yet been discovered in Central America, and the group is unknown, either in the present fauna, or in the fossil state, north of Mexico.

The authors have always included both the neotropical monkeys and those of the Old World in the same zoological unit, to which the same popular name has been applied in various languages (monkeys, singes, Affen, monos, . . .). From a taxonomic point of view, this grouping is quite justifiable, at least typologically, with the condition that Man and the apes be included therein. Indeed, Platyrrhini and Catarrhini show a number of common characters, sometimes complex ones, which set them off from the other Primates. But a problem arises when one tries to be precise with regard to their phylogenetic relationships and their biogeographical history.

The lack of pre-Miocene monkeys in Laurasia forbids us to assume that the Simiiformes might have differentiated there, then to people, in parallel ways, Africa and South America. Two main hypotheses then remain possible: either the presence of monkeys in both southern continents is to be explained by a direct faunal exchange between Africa and South America, across the Atlantic; or the Platyrrhini and the Catarrhini are independently derived from Laurasian "prosimian" stem, which means that their various resemblances are to be interpreted as the results of convergences or parallelisms. The former hypothesis has appeared unlikely in the frame of a fixist paleogeography, so that the great majority of the authors, often reluctantly, has eventually agreed to the latter hypothesis. The resurrection of the theory of the continental drift, and therefore of a mobilist paleogeography was needed before the choice could be contemplated again.

To discuss it, some essential data must be pointed out:

(a) *Branisella*, the earliest Primate known in South America, is represented only by part of the maxillary with some teeth (Plate 1); these show obvious monkey-like characteristics, associated with some archaic features. Morphologically, they are intermediate between those of some Omomyidae and those of modern Platyrrhini, though they are much nearer the latter. The primitive features (P^2 with an unique root, not widened transversally; conspicuous styles on the molars and mostly on the premolars; subtrapezoidal molars, with the hypocones lingually shifted in relation to the protocones) are also found in some Tarsiiformes. But their presence is not surprising at all in an ancient monkey, in the hypothesis that considers a direct derivation from Tarsiiformes, as well as in that which interprets Simiiformes and Tarsiiformes as two sister-groups descended from a common ancestor. As a matter of fact, the molars of *Branisella*, less brachyodont than those of the Eocene Omomyidae, without an external cingulum, with less acute, more bulbous cuspids, with a reduced metaconule, and the protoconule of

Plate 1. *Branisella boliviana* Hoffst., the earliest South American Primate
(early Oligocene of Salla, Bolivia): left maxillary. $\times 8$.





which has disappeared, evoke a monkey much more than a tarsiiform. And the various authors who have considered it (Genet-Varcin, Hershkovitz, Simons) have classified the genus among the Ceboidea. To my mind, it does not seem to be possible to decide, for the time being, whether it is a primitive cebid or whether its peculiar features justify a family (or a subfamily) of its own.

(b) Before the Oligocene, no Primate, nor even any member of the Neotherida*, is known in South America, the ancient mammalian stock of which contains but marsupials and henotherid placentals* (Xenarthra and a complex of ungulates and subungulates). It is only in the Oligocene that the first South American Neotherida appear, with the platyrrhinian monkeys and the caviomorph rodents. The lack of these in earlier levels seems to be significant, notably so for the locality of Itaboraí (late Paleocene of Brazil), situated in the intertropical zone, and which has yielded a rich fauna of small mammals, some of which at least do suggest a forest environment. An indirect evidence may also be found in the fact that the early marsupials of South America have produced small omnivorous-frugivorous (Caroloameghiniidae) and rodent-like types, which suggests the local emptiness of adaptive zones elsewhere occupied by Primates and Rodentia.

So it appears that the Platyrrhini, as well as the Caviomorpha, both having appeared in the early Oligocene, were immigrants. It remains possible, and even likely, that the earliest ascertained forms are not the true founders, and that those may have arrived somewhat earlier, without, however, a considerable time interval being assumed; an immigration dating back from the late Eocene appears very likely.

(c) At the time of these arrivals, South America was separated from all other continents by marine barriers. The Atlantic had already attained an important width, though it was still noticeably narrower than today. An arm of the sea, in the North, occupied the present region of the isthmus (Panama and Costa Rica), and the Bolívar geosyncline too (West of the Western Cordillera of Colombia and Ecuador): the proof of it is given by the presence of marine sediments with faunas indicating a communication between the Atlantic and the Pacific. Moreover, the isolation of South America is also demonstrated by the strongly endemic character of its terrestrial mammals; Platyrrhini and Caviomorpha are the only immigrants to be known between the Paleocene and the late Miocene, and no emigration of South American origin has been discovered during the same period in Africa or in North America. That excludes the hypothesis of a land connection, which, without any doubt, would have occasioned a massive and bilateral faunal exchange. It must be concluded that, whatever their geographical origin, the monkeys (and also the caviomorph rodents) must have crossed a marine barrier to reach South America.

(d) The origin of the Platyrrhini has been looked for in North America, although the only Haplorhini to be known there during the Tertiary are Omomyidae. One must admit that the dental type of *Washakius*, for instance, from the middle Eocene of Wyoming, might represent a suitable ancestral model for *Branisella* (and for most Simiiformes, indeed). But the gap remains wide and no intermediate, which would allow one to argue a direct filiation is known. On the contrary, the later North American forms, from the late Eocene (for instance *Ourayia*) and still more those from the early Oligocene

* For the definition of the terms Henotherida and Neotherida, see Hoffstetter (1971, 1972, 1973).

(*Rooneyia*)* and the lower early Miocene (*Ekgmowechashala*) seem to be engaged in evolutionary paths which do not allow them to be considered as ancestral to the Platyrrhini.

(e) In his new hypothesis, Gingerich (1973) postulates a derivation of the Platyrrhini from Notharctinae, the only Lemuriformes to be known in North America. Far from simplifying the problem, such a phylogeny would compel us to admit other convergences (loss of the lemuroid disposition of the bulla and ectotympanic; acquisition of molars bearing a hypocone from the types with a pseudohypocone), added to those needed because of the ascertained resemblances between Platyrrhini and Catarrhini. As a matter of fact, the gap between the neotropical monkeys and their stem would be considerably widened, without the least intermediate form being known.

(f) It has also been suggested (McKenna, 1967) that, from North American Omomyidae, monkeys might have differentiated in nuclear Central America (then a peninsula of North America), thereafter to settle in South America through transportation by rafting. In that way, the lack of data concerning the necessary intermediate links between North American Omomyidae and South American Ceboidea would be explained. This hypothesis, in itself plausible, is unfortunately not supported by any positive observation. One will even notice that the appearance of *Ekgmowechashala* in South Dakota during the early Miocene would rather provide a negative evidence: for it is a Tarsiiforme, having probably come from the South thanks to a climatic warming-up, which leads one to think that a colony of Tarsiiformes (and not of monkeys) had persisted until then in nuclear Central America. One should compare with South America, where, thanks to the same warming-up, monkeys (*Homunculus*) have been able to reach Patagonia!

(g) There remains Africa. It was the only continent that sheltered monkeys at the time when these have reached South America. They are ascertained in Africa since the early Oligocene, but they had differentiated much earlier. Moreover, their earliest known representatives show characteristics which make them compatible with the Platyrrhini: presence of 3 premolars (in *Apidium* and *Parapithecus*), lack of an ossified external auditory tube (even in the earliest Pongidae, for instance *Aegyptopithecus*: cf. Simons, 1972, Figure 20, p. 65). Therefore, one can no longer invoke such criteria to reject *a priori* the possibility of an African origin of the Platyrrhini. The astonishing resemblance of the petrosal of *Apidium*, figured by Gingerich, with that of the neotropical monkeys must also be stressed (Hoffstetter, 1974); such a resemblance, bearing on a morphologically complex bone, cannot be due to convergence; it may represent the most convincing proof of the kinship between the Platyrrhini and the fossil monkeys from the Fayum. *Branisella*, by the stage of regression of its conules, is rather evolved, more than *Apidium* for instance; but, by the morphology of its P², it is more primitive than all the known monkeys. Thus it would be necessary to reach back before the Oligocene to find a common ancestor to the

* It is obviously erroneously that Simons (1972, p. 178) attributes to me the hypothesis of a possible relationship between *Branisella* and *Rooneyia*. That latter genus, which is not even mentioned in my 1969 note, is excluded from the ancestry of the Platyrrhini by its geological age, the possession of an ossified external auditory tube and perhaps by its dental formula. In 1969, I have willingly abstained from touching the question of the geographical origin of the ancestors of the Platyrrhini, a problem on which R. Lavocat and myself were then at the stage of reflection and exchange of ideas, which has led to several publications since 1970.

Platyrrhini and the Catarrhini, in all likelihood an unknown African monkey from the late Eocene.

From what has been said, it follows that, keeping to paleontological evidence, the African origin of the Platyrrhini is by far the most likely one. The main obstacle is the crossing of the Atlantic. But we have seen that, anyway, the founders of the Platyrrhini had to cross a marine barrier (on natural rafts) to reach South America. It is true that the Atlantic barrier was then considerable, probably wider than that which separated the two Americas*. But the chances of success of a crossing on a raft involve not only the distance to be covered, but also the marine currents. Now, at the epoch we consider, the equatorial current swept the Central American channel from East to West, and thus it constituted an obstacle to a N-S crossing. On the contrary, this same E-W current naturally bore rafts from Africa towards South America.

This does not mean that such a transportation was easy. On the contrary, most "natural experiments" must have failed. But one success was sufficient for a population of African monkeys to become established in South America, there to undergo a local radiation giving rise to the Platyrrhini.

At least, it is a possible explanation. The alternate hypothesis (North American origin) still has its supporters, to whom Gingerich has just rallied with a revolutionary version. It seems to be far less defensible since, anyway, the possible founders would have had to achieve a sea-crossing, too. Moreover, it requires the achievement of such a complex convergent evolution that is rather unlikely.

Other evidence can be drawn from the recent studies by Lessertisseur, Nakache & Petit-Maire (1972, Figure 2) on the cranio-facial characters of the Primates by means of factorial analysis of correspondences. On the cited diagram, which involves 12 variables, the cloud of the Platyrrhini partly overlaps those of the Cercopithecidae and the Hylobatidae, and lies between the Pongidae and the Hominidae (!). Of course such essentially typological works are difficult to interpret from a phylogenetic view point. It is out of the question to infer from them that the Platyrrhini are more nearly related to Man than the Old World monkeys and apes. But it is interesting to note that, apparently, the modern Platyrrhini have remained, on the basis of the features here considered, very near what may have been the common ancestry of apes and Man. That may not be a proof of their African origin, but one will admit that, if the diagram had disclosed a strong divergence between Catarrhini and Platyrrhini, some would not have failed to use it as evidence in favour of an independent origin of the two groups!

Another path of approach concerns the immunological researches on the basis of which Goodman (1972) concludes, "Taxonomic distance tables for anti-ceboid sera reveal the Ceboidea to be closer to catarrhines than to any living prosimian group" (incl. *Tarsius*). This evidence agrees with the hypothesis of a relatively close kinship of the two groups of monkeys. As a matter of fact, such studies mostly result in assessing the relative antiquity of the dichotomies leading to the modern groups. They do not inform us about the "grade" reached by the most recent common ancestor (which could be here an omomyoid or a monkey), nor about the habitat of this ancestor. However, on the same serological bases, some authors think they can calculate the antiquity of a group. Thus Sarich (1970, p.

* It is at least my opinion. However, according to the Eocene-Oligocene maps of Frakes & Kemp (1972), North and South America were then separated by a greater distance than that which existed between Africa and South America at the same time.

195 and letter dated 21 November 1972) takes back the Platyrrhini-Catarrhini dichotomy to 35–40 millions years, that is at the end of the Eocene or at the beginning of the Oligocene, which agrees remarkably well with our own conclusions, but categorically opposes Gingerich's. However, results concerning other groups are divergent, and they incite us to be careful.

The radiation and the expansion of the Platyrrhini have not reached the amplitude of that of the Catarrhini. From the South American intertropical zone, which seems indeed to be their initial habitat, neotropical monkeys have spread southwards, thanks to a warming-up of the climate in the latest Oligocene and the early Miocene. They have also reached Jamaica, probably by rafting sometime during the Neogene, and have become extinct there recently. Their extension in Central America, to the warm lands of Mexico, seems to have taken place later, probably after the complete emersion of the isthmus of Panama (end of the Pliocene), but no fossils are known.

Two main families have differentiated, both of which may be derived from *Branisella*, at least to judge by the dental characters. In the Cebidae, which have retained the initial formula (2133/2133), the hypocone has lined up behind the protocone, so that the upper molars tend towards a quadrangular outline. The Callithricidae, the evolution of which seems to have been ruled by a tendency towards dwarfism, have experienced a simplification: disappearance of the M_3^3 and obliteration of the hypocone, which has given a triangular shape to the upper molars. At least, it is the simplest phylogenetic hypothesis that can be postulated today.

Some fossils are still posing problems. In particular, the M_3^3 might have disappeared in several branches. Thus *Dolichocebus* has been placed among the Callithricidae by Kraglievich on the basis of its dental formula (2132), but Hershkovitz and Simons ascribe to it the formula 2133, and consider that its cranial characters rather put it among the Cebidae. The Jamaican genus *Xenothrix*, known only by a mandible, shows the formula 2132; but its size and its dental morphology lead Hershkovitz to place it in a family of its own, Xenothricidae; thus it would be the end-result of a particular branch, having differentiated in an island habitat, perhaps from Cebidae.

8. Conclusions

Geographical factors played an important part in the history of the Primates. The preceding account has pointed out exclusively northern groups (at least, to judge from known evidence): Paromomyiformes, Adapoidea, Tarsiiformes. Others are essentially or initially austral: Lemuroidea, Lorisioidea, Simiiformes. It is clear that geographical segregation is one of the major causes of their differentiation.

Though fragmentary, paleontological evidence informs us about the intercontinental faunal exchanges in which the Primates have been involved. One can distinguish:

(a) Exchanges between northern continents. They are obvious, between North America and Europe, at the beginning of the Tertiary, principally during the early Eocene, but thereafter they cease (completion of the opening of the North Atlantic). At the same time, the communication between Europe and Asia was cut off (Ouralian sea, or sea of Turgay), but it became reestablished after the early Oligocene (Stehlin's "Great Cut", which coincides with the extinction of the Adapoidea and the Tarsiiformes in Europe). Between Asia and North America, it seems that the Behring "bridge" never was open to the Primates, perhaps because of its high latitude.

(b) Exchanges between southern continents. They have been more difficult, for oceanic barriers were present as early as the Cretaceous. It is clear that the Mozambique Channel had been crossed by the Primates at the beginning of the Tertiary (settlement of Madagascar); it is not even excluded that a later migration in the opposite direction could be at the origin of the African Lorisioidea. We still have no accurate evidence concerning the exchanges between Africa and the Indian plate during the Paleogene. On the other hand, it is very likely that monkeys crossed the Atlantic from East to West to settle in South America about the end of the Eocene.

(c) Exchanges between northern and southern lands. The distribution of the Strepsirhini and that of the Haplorhini compel us to postulate faunal exchanges between Eurasia and Africa at the beginning of the Tertiary. Thereafter Africa remained isolated during the Oligocene, then the alpine folding reestablished communications, thanks to which the Lorisioidea and most families of Catarrhini (including the Hominidae) were able to colonize Eurasia at various times. From South America the Platyrrhini have reached the West Indies by rafting, and they have occupied Central America after (or a little before) the emersion of the isthmus of Panama.

The Southern lands have experienced a more or less lasting isolation, which, for most of them, has restricted their peopling by Primates. Thus, if we disregard the late coming of Man, South America has received but Platyrrhini, Madagascar but Strepsirhini, and the Australo-Papuan region has remained outside the range of the order.

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Une classification des Primates en 3 sous-ordres est adoptée.

Les Paromomyiformes, possiblement issus des Purgatorinae, illustrent une radiation précoce, localisée dans le temps (Crétacé sup.—Eocène) et dans l'espace (Amérique du Nord et Europe).

Les Strepsirhini posent des problèmes phylogéniques: position des Daubentoniidae; position des Cheirogaleidae (possibles Lorisioidea); interrelations des Adapoidea, Lemuroidea et Lorisioidea. Le berceau du groupe se situe probablement en Afrique, qui aurait alimenté des migrations vers l'Eurasie et Madagascar. Ils n'est pas exclu que Madagascar soit à l'origine des Lorisioidea africains.

Les Haplorhini se divisent deux groupes frères, précocement différenciés par ségrégation géographique de part et d'autre de la Téthys. Les Tarsiiformes, exclusivement laurasiatiques, sont peut-être originaires d'Amérique du Nord, mais leurs relations avec les Paromomyiformes restent problématiques. Les Simiiformes (= Anthropeoidea) sont presque certainement originaires d'Afrique. Une migration transatlantique vers la fin de l'Eocène constitue l'hypothèse la plus vraisemblable (ici argumentée) pour expliquer le peuplement de la région néotropicale par les Platyrrhini. Les Catarrhini, d'abord exclusivement africains (la question des fossiles de l'Eocène de Birmanie reste posée), ont envahi l'Eurasie à partir du Miocène (arrivées échelonnées depuis le Miocène moyen) grâce aux nouvelles connexions géographiques résultant de l'orogénie alpine.

*Laboratory of Physical Anthropology,
Faculty of Science, Kyoto University,
Sakyo, Kyoto, Japan*

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The sexual behavior of four troops of wild Japanese monkeys at Jigokudani and at Takasakiyama was observed for about one month during the middle of the breeding season. Sexual behavior was classified into 46 types from the viewpoint of sign behavior, and a catalogue of this was presented. It was shown that there was high correlation between the two most common types of behavior of the male, hindquarters-display and hand-on-back, and subsequent copulation. Seven stages were noticed in the sequence from initial encounter to leave-taking of a consort pair, and these stages were observed in a fairly regular order in the copulatory sequence. There was correlation between male positive attitude toward females and dominance rank order of the male, but was not between copulation and the dominance rank order. Adult females without infant showed and received positive sexual behavior; females who had an infant neither showed nor received the behavior; juvenile females showed but did not receive the behavior. Males showed positive sexual behavior toward females of their own group, but copulation between them was the most scarce due to female refusal.

1. Introduction

Previous studies of the Japanese monkey have been done through the means of feeding the monkeys and by distinguishing all individuals of the troop from the viewpoint of sociology and/or ecology. Studies of the sexual behavior of Japanese monkeys have been made by Mizuhara (1957), and Tokuda (1958, 1961) from a sociological point of view and the study by Hanby, Robertson & Phoenix (1971) is concerned with the relations of age, dominance rank order and factors of the sexual behavior of a free ranging group of Japanese monkeys. Up to date however no attempt has been made to analyze the semiotic nature of sexual behavior and its peripheral fields.

Descriptions and studies of the sexual behavior of genus *Macaca* other than the Japanese monkey, are as follows: on the rhesus monkey (*Macaca mulatta*), Carpenter (1942), Altmann (1962), Hind & Rowell (1962), Conaway & Koford (1964), Kaufmann (1965), Southwick, Beg & Siddigi (1965); on the bonnet macaque (*Macaca radiata*) Simonds (1965); and on the pigtailed monkey (*Macaca nemestrina*) Tokuda, Simonds & Jensen (1968).

On Primate communication there have been several theoretical works and summaries; these were Hockett (1960), Sebeok (1965), Marler (1965), Bastian (1965), Altmann (1967), and Lancaster (1968). Altmann examined the definition of communication. He determined that "social communication is a process by which the behavior of an individual affects the behavior of others." Such behavior can be called sign behavior. Because the study of communication covers a broad field, I had to limit my objective to some extent. It is said that all associated stimuli are signs, however they may not be communicational ones. Sign behavior is therefore limited in its meaning to a behavioral signal used for communication. It can also be said that the sign behavior has a certain pattern in its function. Then sexual sign behavior is further limited to a sexual behavioral signal for communication.

Of each factor in the communication model of Sebeock, it is relatively easy to recognize addresser and addressee and their situation within the sexual context. Therefore, in order to analyze the sexual sign behavior and its circumstances, I took an ethological viewpoint, i.e. I attempted to find out behavioral stages in the sequences beginning with the male encountering the female to ejaculation and leaving. I gathered data on certain behavioral patterns that were repeated at a similar distance, with a similar angle of body axis, and a similar posture and facial expression in similar situations and called these classifiable behavioral patterns of sexual sign behavior. There are some difficulties in advancing a study in which the sign behavior shown is too complex compared with, for example, that of the stickleback. Most of the difficulties involved in this communication study are due to the monkey being a social and higher animal. Because it is a social animal, we must consider such interrelations between individuals as genealogical relations, history of the troop, problems of ontogeny, and so on. Also, because the monkey has an advanced brain, we must consider factors of symbol, delay, flexibility, arbitrariness, etc., in its behavior which are important factors in consideration of the problems of the origin of human language. Further difficulties are caused in carrying out the study of behavior of wild monkeys. Because I did not use experimental methods nor any artificial procedure, I did not understand clearly which factor or factors of such sexual sign behavior functioned. In this paper, therefore, I will show only the catalogue of classified sexual behavior that I could observe. In addition, I will show preliminary quantitative analysis of the context of behavioral patterning in which I shall make clear the relations between each type of behavior and the relations between the frequency of the types of behavior and the genealogical groups. In the future these results will be used as material to analyze behavior semiotically and, used in comparison with other Primates, they will contribute to phylogenetic considerations.

Materials

Shiga A troop in Nagano prefecture and Takasakiyama A, B and C troop in Oita prefecture were studied. Shiga A troop is one of the troops living at Shiga Heights and has fed since 1962 at Jigokudani. At the time of my study, there were about 60 monkeys in this troop. It contained eight adult males older than six years plus two solitary adult males; one of them was found in most of the peripheral part of this troop during my study period and the other was seen only on one day; 21 adult females (older than five years), including eight females with infants and three females who had no young yet; seven older juvenile males (older than three years old); five older juvenile females who had no young yet; 11 younger juveniles and eight infants. There were no five-year-old males, and the one four-year-old male left this troop during my study on 22 November 1971.

Period

There is a clear estrous season in the Japanese monkey, but it varies in the different troops (Kawai, Azuma & Yoshida, 1967). At Jigokudani the season starts in early September and ends in late January. At Takasakiyama, however, the season is about for six months, from November to April. Judging from the data on the delivery rate in the past eight years at Jigokudani, deliveries hit a peak from the end of April to early May. According to Nigi (1971), the pregnancy period of the Japanese monkey is 170–180 days, so that the peak of

conception is thought to be in October and November. Therefore, this study was made at the expected peak of conception from 29 October to 30 November in 1971 with only four days interruption. The study at Takasakiyama started on 11 January 1972, and ended on 7 February.

Method

Usually I recorded types of behavior of monkeys, relative spacing during the action and time using field notes and binoculars. To record facial expressions, I chose the method of checking the components of the face in three or four grades. Checking articles were ears, eyebrows, sight line, mouth, mouth corners, lips and position of the head. For the purpose of aiding these records, I used a 16 mm movie camera, taking 300 m of film in each field. To record sound, I divided the sounds into components of pitch, evocating time, volume, intonation, rhythm, nature and vibration by ear.

2. Non-behavioral Signs of Sexual Activity in Both Sexes

In males

(1) Redness of the face. Although in each individual there is much variability in the facial color from pink to scarlet, without exception the face shows redness. During the whole estrous season the change of facial color was somewhat irregular.

(2) Coloration of the scrotum.

In females

Non-behavioral estrous signs were noted on the rhesus monkey by Carpenter (1942) and on the Japanese monkey by Tokuda (1961). I refer to these signs only briefly.

(1) Redness of the face. All estrous females showed facial redness, but its intensity is variable.

(2) Swelling and redness of the sexual skin. Estrous females display their sexual skin swelling. Swelling and redness are marked particularly in juvenile females, but similar to the rhesus monkey, the swelling of a full adult female ordinarily could not be noted.

(3) Vaginal secretion. Estrous females produce a sharp smelling vaginal secretion, and it can be seen on the spot where they have been sitting.

(4) Attachment of ejaculate or stained genitalia.

These estrous signs are variable in each monkey and there were many cases in which I could not differentiate clearly. Therefore, estrus cannot be recognized only by these signs. As Carpenter (1942) and Tokuda (1961) pointed out, estrus is recognized by behavior and sometimes only by behavior.

3. Classification of Sexual Behavior

The word "sexual behavior" is used in a broad sense. I will define the word to mean the behavior that increases in the estrous season, that is seen in the interactions between males and females, especially in adults, that will lead a pair to copulation, and also to the

behavior that relates directly to copulation. I noted the different types of behavior that I could distinguish to be sexual behavior, and the catalogue of them is given below (Table 1).

(I) Behavior mostly seen in sequences other than the copulatory.

(1) *Tail-raising*. Of males, the adult raises his tail without relation to the dominance rank order. As the male raises his tail, the most colorful part of his body is exposed, i.e. the white parts at the base of the tail and between the ischial callosities, and in contrast with them, the scarlet anus, and though variable in each individual, the pink, red, or purple scrotum. With the female, the red anus is the only colorful point and is also exposed by

Table 1 The catalogue of sexual behaviors.

No. Behavior	Addresser	Addressee	Comment	No. Behavior	Addresser	Addressee	Comment
(1) Tail-raising	M, F			(26) Walking-over	M, F	F, M	*
(2) Testes-lowering	M			(27) Hand-on-back	M	F	
(3) Tree-shaking	M			(28) Sitting-with the-partner	M-F		
(4) Sounds	M, F			(29) Embracing	M, F	F, M	*
(5) Biting	M	F		(30) Standing-by the-side-of the-partner	M, F	F, M	*
(6) Chasing	M	F		(31) Muzzle-to-the-partner	M	F	
(7) Muzzle-to-genitals	M	F		(32) Grooming	M, F	F, M	
(8) Hind-quarters-display I	M, (F)	F, (M)	*	(33) Self-grooming	M, F	---	
(9) Penile erection	M			(34) Presenting	F	M	
(10) Approach	M, F	F, M		(35) Hitting	F	M	
(11) Crouching	F	M		(36) Mounting	M	F	
(12) Kicking	F	M		(37) Pausing	M, F		
(13) Leading-and-following	M, F	F, M		(38) Spasmodic movement	M, F		
(14) Looking-backwards	M, F	F, M	*	(39) Copulation with ventral-posture	M-F		
(15) Attacking-the-third-monkey	M, F	F, M		(40) Pushing male onto the back	F	M	
(16) Head-bobbing	F	M	possible in males	(41) Yawning	M		
(17) Head-ducking	M, F	F, M	*	(42) A female mounting a male	F	M	
(18) Nodding	M, F	F, M	*	(43) A male mounting a male	M	M	
(19) Scratching-the-ground	F	M		(44) A female mounting a female	F	F	
(20) Hand-on-ground	F	M		(45) Male masturbation	M	---	
(21) Beating-the-ground	F	M		(46) Female masturbation	F	---	
(22) Lip-smacking	M, (F)	F, (M)					
(23) Scanning	M, F	F, M	*				
(24) Walking-by	M	F					
(25) Hind-quarters-display II	M	F					

M: male, F: female,

* Intersexual, ---: none of addressee, blank: indistinguishable, (): scarce.

tail-raising. Females do not raise their tails as frequently as the males. The younger the female, the more they raise their tails.

(2) *Testes-lowering*. When walking, males swing their testes. When they run or mount females, they set their testes in the abdominal cavity. The scrotum is beautifully colored when the male is sexually active.

(3) *Tree-shaking*. This behavior is observed in males and is the same as the behavior that Hinde & Rowell (1962) called branch-shaking and Altmann (1962) called shakes limb. A male climbs to a branch which commands the group and shakes the branch by flexing and bending his legs rhythmically. This behavior is not confined only to the branches but in extreme cases the male also leaps and bounds on the ground. Tree-shaking appears to have a relation to social status and probably to the age of the monkey, so that the intensity and frequency of the behavior differs individually. Generally speaking, the older the male, the more tree-shaking he does, and the more sound (mentioned below) he emits. Tree-shaking is rarely shown during the mounting series.

(4) *Sounds*. (4.1.) (*ga.ga.ga.ga. . .*).* In most cases this sound is emitted only by males during tree-shaking. It resembles the sound heard during aggressive chasing,** but the mouth is slightly more open than in the latter case. Lasting time, volume and tone differ for each individual, so the observer could usually distinguish the emitter by sound. At Jigokudani, only males who were older than four emitted this sound. Except with tree-shaking, there was only one case in which it was emitted in the sequence of hindquarters-display I. When a solitary male emits this sound, it is sometimes observed that estrous females are approaching him.

(4.2.) (*hoa, a, ua. . . , uoon*).† Sounds of this group are emitted by females with varying frequency. Eyebrows and eyelids are not moved, mouth is opened, mouth corners are not retreated, lips near the mouth corners are closed, teeth are not exposed, and mouth is slightly protruded. The sound is weak and not high pitched, and its intonation is very variable. This sound may be followed by the 4.3. or 4.5. sounds mentioned below.

(4.3.) (*ugyaaa, gyaaagya, uaaa, ugiiii*).‡ These sounds, emitted by females, are screams and are not clear sounds. Ordinarily this is emitted after a 4.2. sound. Ears are laid back along the head, eyes are ordinarily turned upon a point where there are no other individuals. Eyelids are unstable and vary from open to closed. Teeth are exposed. Mouth corners are slightly brought forward and the part just above the mouth is wrinkled. Most of the time, estrous females emit this sound while alone in a tree.

(4.4.) (*ukyakoko*). This sound emitted by females seems an intermediate of or mixture of the 4.3. and 4.5. sounds. Most of the time it has three "syllables" and the accent falls on the middle "syllable". Eyebrows are unstable and may or may not be slightly lowered, eyelids are opened a little, mouth is opened, and mouth corners are protruded. This sound is emitted when an estrous female is alone or when she starts to approach a male. In the latter case, she switches over to the 4.5. sound.

(4.5.) (*ka.ka.ka.ka. . . , ko.ko.ko.ko. . . , ho.ho.ho.ho. . .*).§ This is a monotonous, hoarse and non-vocal sound made by females. When it is emitted, ears are laid against the head, eyebrows are raised, eyelids are slightly closed, and eyes are not as intent as when staring at a male. Mouth is not as protruded and is more closed than it is in the 4.2. sound.

* C-5 sound.

** C-1 sound.

† E-1 sound.

‡ E-2 sound, from Itani (1963).

§ E-3 sound, from Itani (1963).

Sometimes the upper body is moved up and down rhythmically as the sound is emitted. Sometimes this sound is voiced. The vocal sound seems to be an intermediate sound between typical 4.5. and 4.3. sound. When this sound is emitted the mouth is open more than it is in the typical 4.5. sound, and the sound itself is like the succession of short sounds that are emitted during defensive threat. The 4.5. sound is emitted (i) when a male leaves a female after sitting with her, (ii) when a female clings to a male's back when he stands after sitting with her, (iii) when a female approaches a male, (iv) when a female displays the presentation position or pats the male who is sitting behind her, and (v) in homosexual behavior between females.

(5) *Biting*. A male approaches a female from behind, lowering his body and displaying head-ducking, then, suddenly, he jumps and bites her all over her body. The responses of the bitten female are similar to the responses at ordinal fighting. When the female discovers the male approach, biting does not occur. When the female flees, the male chases her.

(6) *Chasing*. Sometimes males run at and chase females. This behavior is observed before (5), when a female sits with a male and another more dominant male runs toward them, and when a female approaches a subordinate or solitary male. Males sometimes emit sounds (*go.go. . .*) (*ga.ga. . .*) or (*goooo*)* while chasing. After chasing for a while, the male stops. Females are not caught in most cases, but when they are, they crouch and are bitten while in that position. After the chase, the male and female sometimes approach each other, and this results in copulation. Ordinarily, though, they leave each other. There are several cases of a dominant male chasing another male and of a dominant female chasing another female.

(7) *Muzzle-to-genitals*. A male approaches a female and directs his muzzle toward her genitals with his head lowered. Because the female recipient ordinarily shows swelling of her genitals and vaginal secretion, it seems that the male not only looks at the genitals but also smells them. Sometimes males touch the female's genitals. This behavior is shown not only by adult males but also infant, and juvenile males. Ordinarily females show only a slight response, but sometimes they start walking away slowly without fleeing from the approaching male. In the latter case females usually show a defensive facial expression. Seldom are there cases where males grasp and bite or chase females after they have shown this behavior.

(8) *Hindquarters-display I*. This behavior resembles hindquarters-display II which is mentioned later, and is composed of the following chain of elementary types of behavior:

- (a) Staring: a male stares at a female with his body facing her.
- (b) Head-ducking: the male lowers his head to his shoulders and protrudes his mouth.
- (c) Lip-smacking: (mentioned later).
- (d) Turning: the male turns his face away abruptly and then turns his body from his standing point. This results in his hindquarters' being directed toward the female.
- (e) Hindquarters-display: the male stands with his eyes gazing somewhere else, with his tail raised, and with his hindquarters directed toward the female.

Some of these elementary types of behavior may be omitted, so a complete chain of them cannot be seen in most cases.

A behavior similar to this is shown by the female, but it is less ritualized and less frequently observed. I observed only one case during my study at Jigokudani in which the most dominant female behaved in this manner. Basically this behavior should be classified

* C-1 sound, from Itani (1963).

as part of the males repertoire. The main difference between this behavior and hindquarters-display II is the distance between the male and the female. The distance between the sexes in hindquarters-display I is more than that in hindquarters-display II and sometimes extends to more than 50 m. Ordinarily no sound is emitted with this behavior, but there was one case in which it was observed with a 4.1. sound. Rarely after this behavior is shown does the female or the male approach each other and have more intimate relations. This behavior seems to be a self-oriented one to some extent.

(9) *Penile erection*. This behavior is observed in the following situations:

- (i) When infants and/or juveniles are playing.
- (ii) When a female grooms a male.
- (iii) When in the course of a ritualistic mounting between males.
- (iv) When a male sits with a female.
- (v) When a male masturbates.
- (vi) When a male is resting by himself.

This is a self-oriented behavior or reflex. It does not seem to me that this behavior is a display directed toward the other monkeys as in the case of the baboons mentioned by Wickler (1967).

(II) Types of behavior observed mostly in the sequence leading to copulation.

(10) *Approach*. I divide this into five additional types according to approaching speed, posture, and whether or not it was performed directly.

(10.1.) Direct-running-approach. This approach is displayed by males before chasing or attacking females, and by females before jumping on or over males.

(10.2.) Direct-trotting-approach. This approach is slower than (10.1.) and precedes hindquarters-display II.

(10.3.) Direct-walking-approach. This is an approach displayed by males and has somewhat strained steps. This sometimes precedes males standing or sitting in front of females. Also, a female who is consorting with a male may do direct-walking-approach up to the male's back, but its frequency is low. This type of approach usually changes to graduated-walking-approach (10.5.) or to leading-and-following (13).

(10.4.) Stealing approach. This is observed before biting.

(10.5.) Graduated-walking-approach. This behavior is the most common approach by females. When a female approaches a male, she sits behind him, starts walking, then sits, continuing these two motions so that she approaches him gradually. The shorter the distance between the pair is, the less she walks. When the distance between them is very short, she approaches him with her back directed toward the partner. When the male displays this behavior, his body axis does not show correlation to the female body axis nor to the distance between them. This behavior is ordinarily followed by leading-and-following (13).

(11) *Crouching*. This behavior was shown only by juvenile females during my study period. When a male is walking near a female, she approaches and hits him, so that the male looks at her, then she crouches. Her genitals are sometimes directed to him but ordinarily they are vertical to the line which passes through the pair.

(12) *Kicking*. This behavior is observed only in juvenile females. They approach males, abruptly kick them with their hind legs, then flee.

(13) *Leading-and-following*. This is the behavior in which both males and females walk

around leading and following in turn. It is composed of three elementary types of behavior, i.e. sitting, walking away or leading, and approaching or following. This behavior is ordinarily followed by sitting-with (28). I divide this behavior into three types according to which sex has the initiative.

(13.1.) Males following females. The dominant male follows some females who are in estrus in the highest degree and continues this behavior for a few days. No copulation was observed between these individuals. Ordinarily other males follow these pairs, and the dominant male sometimes threatens them.

(13.2.) Females following males. This case sometimes results in copulation, but sometimes the male threatens the female. However, once they copulate, in most cases the male no longer threatens the female.

(13.3.) Mutual leading and following. After this the frequency of the sequence resulting in copulation is highest. Leading and following, including sitting-with, results more in the next stage which is represented by sitting-with, than in other cases.

(14) *Looking-backwards*. This behavior is shown by the leading monkeys of both sexes during leading-and-following, or by monkeys when they are passing each other. It appears that in looking back, monkeys can assess the circumstances behind them. This behavior seems to be an invitation sign for another monkey to approach.

(15) *Attacking-the-third-monkey*. This behavior is shown by both sexes although the situations in which the behavior is seen is different in each sex.

(15.1.) Females attacking. When a female continues consort relation with a male (i.e. relation in which both sexes continue to keep a short distance between them), or before a female has sexual relations, she attacks a third monkey. In a situation where she attacks a male, she approaches the male gradually, sometimes looking over her shoulder at her partner. Her posture is of ready flight, facial expression is what can be called "eyelids display" and she emits the sound (*ho.ho.ho. . .*)*. The attacked male shows her a threat expression then walks away. Sometimes the male attacks the female back. In such a case, her partner attacks and/or chases the attacking male. This behavior is presupposed to be the males protective reaction because the female is basically subordinate to the attacked male. Therefore the object of her attack is restricted to a male who is subordinate to her partner.

Attacking the female is shown in the situation where another female (second female) approaches the male of the pair. In this situation the female of the pair (first female) does not show "eyelids-display" but shows instead the facial expression seen during aggressive encounters between females and attacks. If the second female dominates the first female, when the second female counter attacks, the first female hides behind the male. If the male does not protect the first female by threatening of chasing the second female, the second female occupies the position of the first female.

(15.2.) Male attacking. When a dominant male approaches the pair and sits near them, the female of the pair walks a few meters away from her partner. The male of the pair threatens a third, subordinate male mostly with a facial expression like "eyelids-display" although the eyelids are less closed. This behavior is not seen all the time in this situation.

(16) *Head-bobbing*. In this behavior the monkey raises its head abruptly staring into the eyes of its partner.

(17) *Head-ducking*. In this behavior a monkey abruptly lowers its head to its shoulders and stares at its partner.

* Like C-2 sound, from Itani (1963).

(18) *Nodding*. A monkey shakes its head up and down while in a sitting or standing position. The line of vision is directed toward the partner while bringing the head down but not when the head is lowered. This is observed when a male and a female sit within a short distance of each other. Frequency of this behavior is low. When a female displays this behavior to a male who is not in consort relation with her, he will usually chase her. A male nods his head when he embraces a female, like a female does when she embraces her infant.

(19) *Scratching-the-ground*. This is a behavior seen in females. A female in a sitting position scratches the ground from front to back with her hand while staring at her partner. Sometimes her hand does not touch the ground, while at other times she scratches the ground from the side to the front of her body.

(20) *Hand-on-the-ground*. This behavior is also found in females. She puts her hand on the ground in front of her and brings her center of gravity forward onto her arm as if she is starting to walk. Eyes are directed toward the partner.

(21) *Beating-the-ground*. This behavior is seen in females. A female beats the ground in front of her with her eyes directed toward her partner.

(22) *Lip-smacking*. In this behavior the mouth is protruded and the lips are rapidly smacked. Position of eyebrows and upper head skin vary according to intensity, from having eyebrows that are not raised, to eyebrows that are a little raised, but upper head skin is not raised, to where both eyebrows and upper head skin are raised. Ears are laid against the head. Eyes are directed at a female with eyelids are not fully opened, blinking also sometimes accompanies this. The head is lowered a little sometimes. At sexual encounters this behavior is performed by males toward females, and is shown (i) when a male sees a female who is far away from him and displays head-ducking to her, (ii) at hindquarters-display, and (iii) during or before grooming. In the last situation however the rate of smacking is slower than case (i) and (ii).

(23) *Scanning*. This behavior is seen in both sexes. From a short distance a monkey stares at its partner while lowering its head. Sometimes, though, the head is not lowered. This behavior is often accompanied by (22). It is seen (i) just before the male walks a short distance away after having started the mounting series with a female, (ii) just before mounting, (iii) at hindquarters-display II and (iv) when a female scans a male while sitting with him.

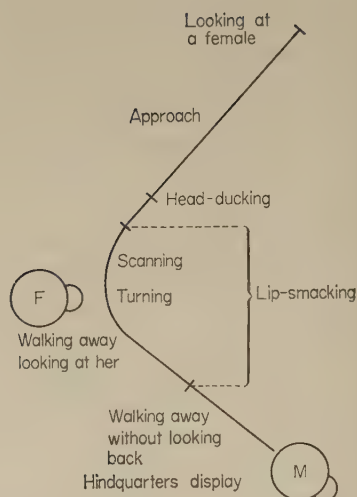
When males scan females, females sometimes show a defensive expression. When females scan males, males commonly turn their faces away.

(24) *Walking-by*. In this behavior a male approaches a female and walks by her at a short distance. Sometimes his fur touches her fur. He continues walking in the same direction. Part of the behavior (25) is sometimes shown after this.

(25) *Hindquarters-display II*. This is one of the most common acts displayed by males. It is composed of nine elements and is shown in a fairly regular chain as follows:

- (a) From a varying distance he looks at a female.
- (b) He approaches her using the direct-walking-approach.
- (c) He displays head-ducking before her and protrudes his muzzle.
- (d) He scans her face.
- (e) He displays lip-smacking while staring at her.
- (f) He turns in front of her.
- (g) He walks away, still looking at her.
- (h) He walks away without looking back at her.

Figure 1. Hindquarters-display I.



(i) He stands and shows his genitals to the female with his head lowered, eyes staring and tail cocked. (Figure 1)

The distance between the male and the female is ordinarily 0–2 m and the angle of the line between the male and the female and the male's body axis is 0–30° [Figure 2(a, b)]. From this I conclude that the male is finally displaying his genitals to the female. The frequency of these five of the eight elementary types of behavior leading to hindquarters-display is fairly high without lip-smacking. This fact shows that these elementary types of behavior appear in the set [Figure 2(c)]. But there are other cases observed, for example, when the male walks over the female's back, or puts his hand on her back before displaying his genitals, and when this behavior is shown during intermittent mounting series. The female responds to hindquarters-display II by beginning to sit and, if she is eating something, she finishes it showing a defensive expression or by beginning to walk away. In most cases she does not look at male's sexual skin.

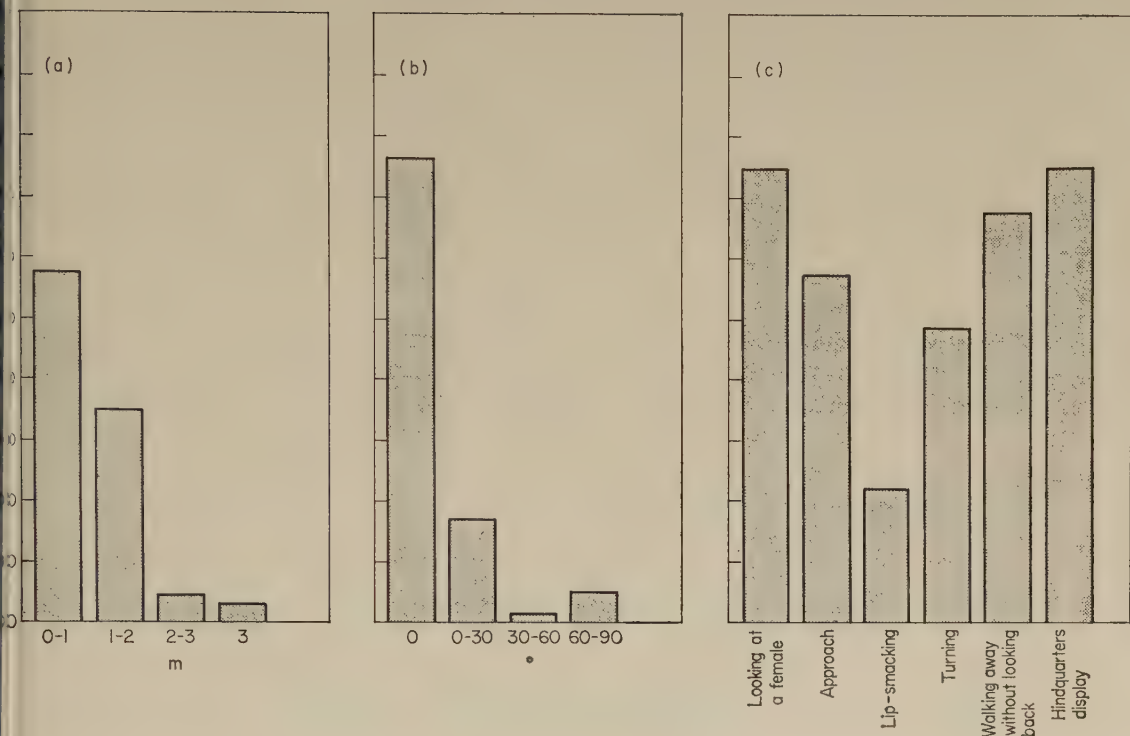
(26) *Walking-over*. A male puts his hand on the back of a female, jumps onto her back, kicks her there, and then walks away. After walking over her he sometimes displays behavior (25). This behavior is also shown by females.

(27) *Hand-on-back*. A male approaches a female who is sitting or standing and lightly puts his hands on her middle of lower back; sometimes though, he does this with force. This is done with both palms and back of the hands. There are several other cases in which he grasps her back and in extreme cases he pulls the fur on her back. Hand-on-back is shown before starting the mounting series. The female response is variable. When both sexes are staying in close proximity and are preceding through the stages, which will be mentioned later, in proper order, she looks back at the male or shows half standing posture. But when the male grasps her back and/or pulls her fur, she shows the facial expression of fear, then shows the posture of ready flight, and sometimes she actually does flee.

Hand-on-back could also be observed in the female. Excluding the display a female shows just before mounting a male, this behavior is shown by a juvenile who cannot fulfill her sexual motivation.

A type of behavior similar to this is observed at mounting and will be mentioned later. But the "putting hands on the back" in mounting is performed less with the palms and with less motion than in this case.

Figure 2. (a) The distance between male and female during the hindquarters-display. (b) The angle made of a line which links the male and female and male's body axis during the hindquarters-display. (c) The rate of appearance of elements of the hindquarters-display.



(28) *Sitting-with*. This occurs when a male and a female sit within a short distance of each other. Operationally I took sitting within 1 m of each other for the standard but once and awhile they sat at a distance of 2 or 3 m. Before copulation they seldom face each other. The female sits with her side or back to the male.

(29) *Embracing*. When a male and a female sit together, they sit with their bodies touching, lightly holding each other. In most cases embracing is seen during the mounting series or just before and just after the mounting series.

(30) *Standing-by-the-side-of-the-partner*. (30.1.) Turning to face the partner. This is shown by both sexes at the sitting-with stage. There are two common ways in which this occurs. In the first, when the female stands and moves to face the male, he reorients his body axis to avoid sitting face to face with her. In the other, when the female is sitting with her back to the male, she turns around to look at him and they embrace each other. When the female takes her position in front of the male, and he does not reorient, they begin the mounting series.

(30.2.) Standing at the side of the partner. At the sitting-with stage a male or a female sometimes stands by the side of the partner.

(31) *Muzzle-to-the-partner*. Usually monkeys touch their muzzles to another monkey's muzzle, but sometimes they muzzle their partner's back, and neck. This is shown at (25) or at (28).

(32) *Grooming*. This is shown from the unstable leading-and-following stage to the mounting stage. A female grooms a male more than in the reverse case. Sometimes the role of groomer is exchanged.

(33) *Self-grooming*. This is shown in the same situation as (32).

(34) *Presenting*. This female behavior resembles that of the male's hindquarters-display II (25). A female backs up to a male with her hindquarters toward him and with her tail raised looks at him over her shoulder. The distance between the two monkeys is less than 1 m during this behavior, and in extreme cases the female's hindquarters touches the male's body. The male's body axis is variable.

(35) *Hitting*. When the female is sitting in front of or by the side of the male, she hits his side with the back of her arm or hand. Sometimes this behavior is also shown during the mounting series.

(III) The copulatory behavior.

(36) *Mounting*. Males mount females repeatedly with intervals of tens of seconds and finally they ejaculate, completing the copulation. This is commonly composed of a chain of several elementary types of behavior (Table 2). In the types of behavior that are shown

Table 2

Mounting

Male	Female
(Sitting)	(Sitting)
Putting hand on her back	
	Standing
Putting hand on her back again	
Pelvic thrusts	Seeing male over her shoulder*
	Grasping male's body*
Pausing**	
Dismounting	
Sitting	Sitting

* not always.

** only last mounting.

just before mounting, the most common is "putting hands on the back". Other types of behavior than this are very variable (Table 3). At the early stages of the mounting series pelvic thrusts can occur without the penis entering the vagina. In this case, the male pushes the vagina with his penis, but does not perform strong pelvic thrusts, movement of his pelvis is little, and the periodic timing of the thrust is short. As he inserts his penis, he thrusts his pelvis with variable force, and his tail swings up and down. The female secretes more and more liquid from her vagina. The last mounting, including ejaculation, has the maximum number of thrusts (Table 4). Ejaculation is usually observed during the last mounting, although there are some cases observed in which ejaculation is shown earlier.*

Juvenile males make less thrust movement than adult males and the periodic thrust rate is irregular. Sometimes partners of juvenile males show positive behavior such as (4.5.), (35), and (40).

* Excepting the last mounting, I observed that in 19.3% of the copulations at Jigokudani and 24% at Takasakiyama ejaculate fell from the penis just before it was inserted into the vagina.

Table 3

The behavior just before mounting. Observed copulations were 26 at Jigokudani and 48 at Takasakiyama, and types of behavior were counted when they were observed during copulation

Actor	Behavior	Jigokudani		Takasakiyama	
		No. of copulations with the behavior	%	No. of copulations with the behavior	%
Male	Hand-on-back	26	100	48	100
	Grasping back	2	7.7	9	18.8
	Standing	5	19.2	20	41.7
	Turning	1	3.8	1	2.1
	Approach	1	3.8	4	8.3
	Spasmodic movement	16	61.5	1	2.1
	Seeing backwards	2	7.7	0	0
	Pulling	0	0	4	8.3
Female	Standing	3	11.5	10	20.8
	Hand-on-ground	0	0	2	4.2
	Spasmodic movement	3	11.5	1	2.1

(37) *Pausing*. During the time between mountings, the pair sit together quietly within a short distance of each other. There is other behavior observed than this. Types (32) and (33) are the most commonly displayed by both sexes.

(38) *Spasmodic movement*. Both sexes sometimes show abrupt spasmodic movement shortly before and during the mounting series. This seems to be related to penile erection if occurring in the male.

(39) *Copulation with ventral-ventral posture*. This type of copulation posture is ordinarily observed in pairs of juveniles. The male displayed pelvic thrusts but it was not clear whether or not he inserted his penis into her vagina. The male does not ejaculate in this posture.

Table 4 Elements of copulation

Element of copulation	Mean	Range	S.D.	No. of cases
(a) Length of copulation	8 min 54 sec	2 min 50 sec–32 min 47 sec	7 min 22.4 sec	44
(b) Number of mountings in a copulation	14.8	4–45	9.5	44
(c) Mean length of intervals	35.7 sec	19.7–65.1 sec	11.7 sec	44
(d) Total number of thrusts in a copulation	24.6	4–53	12.6	31
(e) Maximum number of thrusts without last mounting	2.9	1–6		31
(f) Thrusts of last mounting	4.3	0–6		31
(a) Length of copulation	10 min 54 sec	3 min 36 sec–23 min 17 sec	5 min 59.2 sec	24
(b) Number of mountings in a copulation	18.9	5–45	10.5	26
(c) Mean length of intervals	38.1 sec	22.6–64.5 sec	8.5 sec	26
(d) Total number of thrusts in a copulation	35.9	9–72	21.2	21
(e) Maximum number of thrusts without last mounting	3.5	2–5		21
(f) Thrusts of last mounting	5.2	1–7		21

(40) *Pushing-male-onto-the-back*. A female who copulates with a juvenile male sometimes pushes him onto her back.

(41) *Yawning*. This is composed of two phases. First, the mouth is opened in the shape of an upright enlarged oval. Because mouth corners are brought forward, teeth are not exposed. Then mouth corners are pulled backward, so that teeth and gums are exposed. This is observed frequently in the copulatory sequence.

In Table 4 I show each of the elements involved in copulation. Although there is not much difference between the two populations, the values at Takasakiyama are larger than at Jigokudani for each element. There is also much variety in each element. The elements in reference to each adult male at Jigokudani appear to have no correlation to dominance rank order although I cannot definitely assert this because observed cases are few and have much variety (Figure 3). But in the observations of males of numbers 1, 2, 4 and 5, whose cases were relatively many, it is clear that the minimum length of time taken to complete copulation, the number of mountings per copulation, and the maximum length of interval time between mountings in a copulation show a tendency to be equal. It seems that to maintain or complete copulation monkeys require more than 5–7 min in copulation time, more than 5 mountings in a copulation and less than 65 sec in interval time between mountings in a copulation.

(IV) The other types of sexual behavior.

This category includes homosexuality, inverted heterosexual behavior and autoeroticism. I will not describe these types of behavior in detail in this paper. Briefly they are as follows:

(42) A female mounting a male.

(43) A male mounting a male.

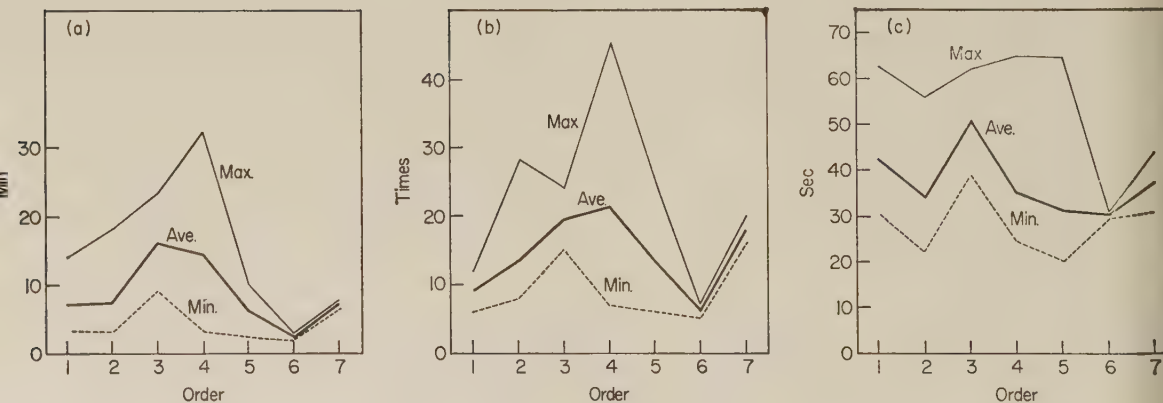
(44) A female mounting a female.

These three types of behavior are often finished quickly without a long time.

(45) Male masturbation (rubbing his penis with his hand).

(46) Female masturbation (rubbing her genitals against something).

Figure 3. (a) The relation of length of copulation to dominance rank order of the male. (b) The relation of the number of mountings during copulation to dominance rank order of the male. (c) The relation of mean length of intervals during copulation to dominance rank order of the male.



4. Consequential Analysis of Two Types of Behavior: Hindquarters-display and Hand-on-Back

Two types of behavior shown by males, hindquarters-display and hand-on-back, are observed in highest frequency in the copulatory sequences. The relations of these two types of behavior to subsequent copulation are shown in Table 5. According to this table, cases

Table 5. (a) The relation of hindquarters-display to subsequent copulation. (b) The relation of hand-on-back to subsequent copulation.

		Copulation	Number of cases	%
	(a) Hindquarters display			
(a)	Y	N	7	21.2
(b)	N	Y	6	18.2
(c)	Y	Y	20	60.6
				$\frac{(c)}{(b) + (c)} \times 100 = 74.1$
	(b) Hand-on-back			
(a)	Y	N	4	13.3
(b)	N	Y	17	56.7
(c)	Y	Y	9	30.0
				$\frac{(c)}{(b) + (c)} \times 100 = 34.6$

Y: the behavior was observed, N: the behavior was not observed.

in which copulation was observed after hindquarters-display are much more frequent than cases in which copulation was not observed after hindquarters-display or cases in which copulation was observed without hindquarters-display preceding it. These differences are significant at a 2% level of the chi-square test. Although the relation is less than in hindquarters-display, a similar relation can be seen between hand-on-back and copulation at a 26% level of the chi-square test. Therefore, I can say that hindquarters-display and hand-on-back have an intimate relation with copulation.

However, this does not necessarily mean that these two types of behavior trigger copulation, because both these behaviors can be seen in the earlier stage of copulation.

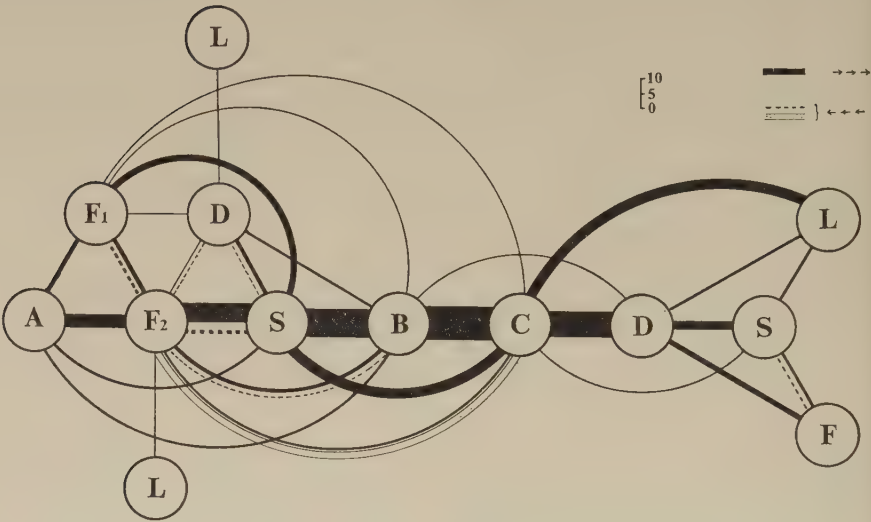
5. Structure of the Copulatory Sequence

There are three common types of sexual interaction between the sexes. In one, a male one-sidedly follows a female showing several types of behavior such as (27) or (25). In a second, a female one-sidedly follows a male. In the last both sexes participate. Only in the last type does the sequence end in copulation.

In the last type of interaction, taking the distance between the pair and time for the variables, about six stages can be admitted to the sequence from encounter to copulation to leaving the partner. These are equated to behavioral interacting patterns. The stages were observed in fairly regular order as seen in Figure 4.

Considering this and Table 6 that shows in which stages the behavior appears, the structure of the standard sequence including copulation appears to be as follows: first, a

Figure 4. The sequence of sexual behavior. A: approach, F₁: leading-and-following (there is not a chance sitting together within 1 m), F₂: leading-and-following (there is a chance sitting together within 1 m), D: sitting together without 1 m, S: sitting together within 1 m, B: early stage of copulation; it is not stable, C: stable stage of copulation, F: leading-and-following after copulation, L: leaving.



male or a female approaches the other with a gradually-walking-approach. Then they lead and follow each other, gradually shortened until finally they sit very close together. He may again show hindquarters-display. He puts his hand lightly on her back, they turn, he goes behind her back and pushes it with his hands. She stands and the mounting series starts. She grooms him. He may walk away a little or may interrupt mounting or pelvic thrusting and show hindquarters-display to her. But gradually such types of behavior are diminished, and mounting is repeated until he ejaculates with convulsions in the hind legs and with his tail down. Dismounting, he walks a few meters away, self-grooms, yawns and/or eats coagulated ejaculate that he removes from his penis. Then, one of them approaches the other and sits with him/her, and they enter into the stage of leading-and-following, or one leaves the partner. If they do not leave each other the sequence continues again to copulation.

Table 6 Order of appearance of ten types of behavior

Stage	A	F ₁₊₂	S	B	C	D
Seeing-backwards		_____				
Yawning			_____			
Scanning			_____			
Lip-smacking		_____				
Muzzle-to-muzzle		_____				
Walking-over		_____				
Hand-on-back		_____				
Hindquarters-display		_____				
Grooming		_____				
Self-grooming			_____			

These chains of behavior seem to occur in a flow which gradually advances toward the goal of ejaculation. When this flow is cut off by some cause, the pair do not continue their relation at the interrupted stage and do not advance to the next stage, but start again from the earlier stage.

6. The Relations of Social Status to Copulation, Approach-or-Follow, and Hindquarters-Display

The higher the male in the dominance rank order, the higher the frequency of approach-or-follow and hindquarters-display by the male to females as shown in Figure 5(c, d). On the other hand as shown in Figure 5(a, b), the approach-or-follow by females to males and copulation does not show clear correlation to dominance rank order. It may be said that juvenile males do not receive female approach-or-follow and that adult males received this behavior independently of his dominance rank order. According to Figure 5(a), lower ranking adult males and juvenile males did not copulate often and that males over five in the dominance rank order copulated with females independently of their order. The correlations between this behavior and age is not clear.

Also the correlation of female dominance rank order to frequency of copulation, approach-or-follow, and hindquarters-display is not clear from this data [Figure 6(a-d)]. Generally, females of middle rank copulated the most, followed by females of higher rank. The females of lower rank copulated the least. It is still not clear, however, that there is a correlation between dominance rank order and the amount of intercourse for females.

Next, dividing the females into three groups according not to their genealogical relations but to their female state: they are mothers (females who have an infant younger than

Figure 5. (a) The relation of copulation to dominance rank order of males. (b) The relation of approach-or-follow by females to dominance rank order of males. (c) The relation of approach-or-follow by males to dominance rank order of males. (d) The relation of hindquarters-display to dominance rank order of males. Numbers were counted one for an individual in a day.

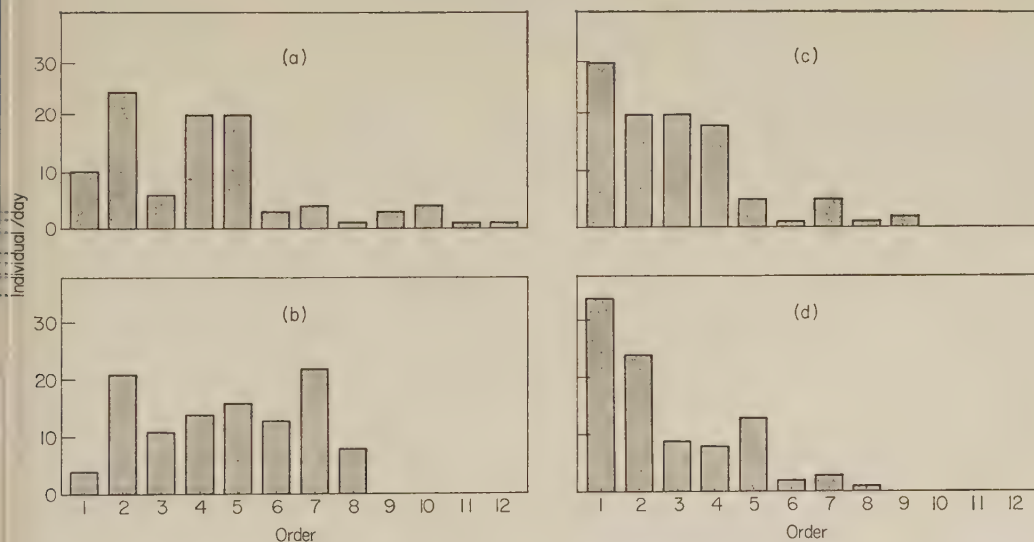
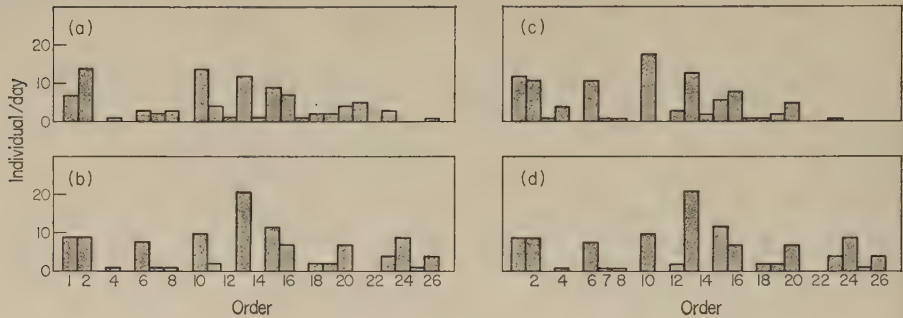


Figure 6. (a) The relation of copulation to dominance rank order of females. (b) The relation of approach-or-follow by females to dominance rank order of females. (c) The relation of approach-or-follow by males to dominance rank order of females. (d) The relation of hindquarters-display to dominance rank order of females. Numbers were counted one for an individual in a day.



one-year-old), adult females without infants, and juvenile females. Comparing these three groups with each other in frequencies of copulation, approach-or-follow by both sexes, and hindquarters-display by males, adult females without infants showed the highest frequency in all four types of behavior, juvenile females showed low frequency in all types of behavior except approach-or-follow by females to males, and mothers showed low frequency in all types of behavior (Table 7).

Table 7 The relation of the four types of behavior, (a) copulation, (b) approach-or-follow by females, (c) approach-or-follow by males, and (d) hindquarters-display, to the female status.

Status		No. of individual	Mean	S.D.
	(a) No. of copulation			
F	76	13	5.8	4.8
M	15	8	1.9	1.8
J	6	5	1.2	1.2
	(b) No. of approach			
F	89	13	6.9	5.5
M	2	8	0.3	0.4
J	18	5	3.6	3.0
	(c) No. of approach			
F	95	13	7.3	5.3
M	5	8	0.6	0.7
J	1	5	0.2	0.4
	(d) No. of hind-quarters-displays			
F	94	13	7.2	7.6
M	8	8	1.0	1.2
J	2	5	0.4	0.5

F: adult females without infant, M: mothers (having infant younger than one), J: juvenile females (younger than four years old), numbers were counted one for an individual in a day.

7. The Relations of Genealogical Groups to Copulation, Approach-or-Follow, and Hindquarters-Display

At Jigokudani the first three males in the dominance rank order belong to the Tomoe genealogical group. Males of the other genealogical groups left the growing troop before becoming adult, and in their place, males number 4 to 8 have entered this troop from the other troops.

Females of this troop belong to five maternal genealogical groups. From these, I selected the three largest groups to analyze the relation of genealogical groups to copulation, approach-or-follow and hindquarters-display; they are the Tomoe group (T group), the Muku group (M group), and the Saku group (S group). Because of reasons mentioned earlier, this category of females does not include mothers or juveniles. Males who have come from outside troops are grouped together (O group); all adult males except those of the T group are included in this group.

Females of the T group copulated more with O group males than with males of their own group. On the other hand, females of the M group copulated more with T group males than with O group males, and females of S group copulated as much with T group males as with O group males [Table 8(a)].

As indicated in Table 8(b), T and S group females displayed approach-or-follow more to O group males than to T group males, but M group females displayed a reversed tendency in this behavior.

According to Table 8(c), the higher ranked T group males displayed more approach-or-follow to females than the subordinant O group males, therefore the ratio of the T group

Table 8 **The relation of the four types of behavior, (a) copulation, (b) approach-or-follow by females, (c) approach-or-follow by males, and (d) hindquarters-display, to the genealogical group. Figures are the quotient of actual observed number in Table 8(a) or of the number counted one for an individual in a day in Table 8(b-d) divided by number of combinations between males and females of the groups**

Male Female	T group	O group	ratio T/O	ratio (T)/(O)
			(a)	
T group	0.83(22)	1.05(45)	0.79	0.49
M group	2.33(63)	0.73(31)	3.19	2.03
S group	0.56(15)	0.57(24)	0.98	0.63
			(b)	
T group	0.50(19)	1.10(37)	0.45	0.51
M group	1.89(71)	1.07(36)	1.77	1.97
S group	0.28(10)	0.80(27)	0.35	0.37
			(c)	
T group	2.25(40)	0.55(35)	4.09	1.14
M group	2.56(45)	0.73(47)	3.51	0.96
S group	0.83(15)	0.27(18)	3.07	0.83
			(d)	
T group	0.25(22)	0.25(15)	5.00	1.47
M group	1.56(62)	1.27(74)	2.80	0.84
S group	3.94(16)	0.27(12)	4.70	1.33

(): percentage, ()/(): ratio of percentage.

to the O group number is higher in all three female groups. Although it can be observed that T group males displayed approach-or-follow to T group females more often than to M and S group females, O group males displayed this behavior to all three groups indiscriminately.

In hindquarters-display, T group males showed this behavior to M group females more often than to females of any other group. This tendency is even clearer with O group males [Table 8(d)].

According to these results, in the interactions of males and females of the T group, the males showed positive behavior to the females, but the females did not show positive behavior to the males. Therefore, the fact that there was less copulation between individuals within the T group was not due to lack of male desire, but to female refusal to copulate with them. Females of the M group had more intimate relations with males of each group. Males of the T group showed the positive types of behavior to females of the S group, and the number of copulations between these two groups showed the mediate value between the T and M group. These facts also suggest that incest avoidance is performed not only by males leaving a troop but also by female psychological avoidance of copulation with males of her own genealogical group.

8. Discussion

Fixed action pattern of male behavior

Copulatory behavior is itself composed of a few types of behavior. Hand-on-back which is seen before starting copulation is very similar to the first part of a mounting. This behavior is clearly "intention movement" (Hinde, 1966) only and the degree of ritualization is not on a high level. Within the copulatory behavior of the male there is no behavior similar to hindquarters-display. During this sequence, behavior such as displaying hindquarters to the partner is basically the behavior of the female. This behavior is probably "displacement activity" (Hinde, 1966), but its origin cannot be solved at this point. At this point I can only say that this is a more ritualized behavior than hand-on-back. Both these types of behavior are part of a fixed action pattern which appears in a similar way in high frequency before copulation.

That there is much appeasement behavior and fixed pattern behavior seems to be based on the dominant male position in relation to the female. In non-breeding season, there is little sexually related interaction. Behavior such as grooming or sitting-with occurs only a few times and only in established pairs. On entering the breeding season, the contact between males and females is desired. Males must show females appeasement behavior to diminish the female fear of the male. Because there is a relation between female fear and the dominance rank order of the male, the higher ranked male shows more appeasement behavior than the lower ranked male. There is a positive correlation between the dominance rank order of the male and several types of positive behavior. Male dominance over the female is desired to show this behavior. The fact that the hindquarters-display I was only displayed by the number one female supports this interpretation.

Though aggressive actions such as chasing or biting can be seen in the male during breeding season, many times there can also be seen an appeasement factor such as lip-smacking during the copulatory sequence. Hindquarters-display II, one of the most frequent types of sexual behavior, is almost always accompanied by lip-smacking, and is also considered to be an appeasement factor.

Arbitrary behavior of the female

The female, on the other hand, has no such fixed action pattern as the male. After she receives hindquarters-display II, whether or not copulation takes place seems to be determined by her. A female can refuse the male by continuing to sit after receiving the display, or walking away. Behavior outside the basic pattern such as scratching-the-ground, hitting, beating-the-ground and, in extreme cases, kicking by females to males belongs more to the category of aggressive behavior than does male behavior that is outside the basic pattern. In frequency none of them equalled males' hindquarters-display or hand-on-back and each behavior was observed in only a few cases. At the same time, in each individual there were many variations in the kind and frequency of behavior. This indicates that the females positive sexual activity seems fairly arbitrary in its appearance contrary to the males fixed action pattern in the copulatory sequence.

Copulatory behavior

It was mentioned that the frequency of male copulatory behavior is related to dominance rank order by Tokuda (1961) and Hanby, Robertson & Phoenix (1971) in the Japanese monkey and by Carpenter (1942), Altmann (1962), Conaway & Koford (1964) and Kaufmann (1965) in the rhesus monkey. This is supported also from the results at Jigokudani about the approach-or-follow by males to females and male's hindquarters-display. But there is not a clear correlation between frequency of copulation and male's dominance rank order. Therefore it can be said that there are other factors which affect the frequency of copulation.

Hanby, Robertson & Phoenix (1971) pointed out that in females having an infant younger than one year and in young females the frequency of copulation was low. This was supported by the troop at Jigokudani. The reasons for the low frequency are different. Females with an infant displayed no positive sexual behavior toward males, while juvenile females did to some extent display positive sexual behavior. In both cases males showed no interest.

9. Summary

From the viewpoint of sign behavior, sexual behavior of Japanese monkeys was broken down into 46 types. Elements of copulation (i.e. number of mountings in a copulation, length of interval between the mountings, and length of time involved in a copulation) were shown. From this paper it appears that none of these elements have a correlation to male dominance rank order. The most frequent types of behavior by males of hindquarters-display and hand-on-back have an intimate relation to the copulation. The structure of the most common copulatory sequence is as follows: first, one monkey approaches a monkey of the opposite sex, the pair lead and follow each other for awhile, then sit together. The mounting series starts, but it is unstable. Gradually it becomes stable, and the male ejaculates during later mountings. The male dismounts and goes a few metres away from the female. It was also shown in which stage different behavior appeared. Of the four types of behavior of (i) hindquarters-display, (ii) approach-or-follow by males to females, (iii) approach-or-follow by females to males, and (iv) copulation, there was correlation between (i) and (ii) only to the dominance rank order of the male. But there were not any clear correlation between these four types of behavior and

dominance rank order of females. Adult females who had infants displayed a low frequency in all four types of behavior; juvenile females showed higher frequency only in (iii); adult females without an infant showed the highest frequency in all four types of behavior. Males showed the positive behavior of both (i) and (ii) to females of their own genealogical group, but females seldom showed positive behavior to males of their own group. It was discussed that hindquarters-display is both part of a fixed action pattern and also an appeasement behavior and why this behavior is specific in males. Also it was discussed that some positive female behavior is arbitrary in appearance.

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B. A. Wood

Department of Anatomy,
Charing Cross Hospital Medical
School, (University of London),
Fulham Palace Road,
London, W6 8RF

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accepted 27 March 1974

Olduvai Bed I Post-cranial Fossils: A Reassessment

New fossil specimens can be interpreted as strong indications that there were two Plio-Pleistocene hominid post-cranial morphotypes. This new evidence may alter the functional interpretations placed on the important specimens, OH 8 and OH 10 from Olduvai Gorge, Tanzania. When these interpretations are critically examined there is now doubt that the OH 8 foot belongs to *Homo* and that the OH 10 terminal phalanx is necessarily part of a functional limb complex like that of modern Man.

Various claims and suggestions have been made in the past about hominid locomotor patterns on the basis of post-cranial fossils from Bed I at Olduvai Gorge. Using anatomical features to draw analogies with modern gait patterns is acceptable if the fossils are part of a morphological continuum and if this continuum can be traced to the extant groups with which the fossils are being compared. This type of process is distinct from the recognition of homologous features, for these though homologous in structure are not necessarily so in function.

There is now, however, fossil evidence, controversial though it is, for a second hominid post-cranial morphotype. Post-cranial fossils from Swartkrans (Napier, 1964), and Olduvai (Day, 1969), were considered to be morphological distinct from modern hominids. There was until recently no indication that they represented more than a stage in the development of the modern human pattern. More recent evidence from East Rudolf (R. E. F. Leakey, 1973), suggests that this pattern was not sequential but was sympatric with material that is much closer to the modern human morphology. It is therefore apparent that assumptions which were justified before this evidence was available may not necessarily be valid now.

The present relative abundance of post-cranial fossils has reduced the pressure to make locomotor predictions from material that is often less than ideal for the purpose. Those who are concerned with early hominid evolution are naturally anxious to reconstruct all aspects of behaviour. As locomotor capabilities are widely considered to have played a key role in the biological success of hominids, functional interpretation of post-cranial material has been keenly pursued. However such interpretations, whether correct or not, can introduce circular reasoning into the assessment of fossil evidence. Even though they are rarely included in the diagnosis of taxa there are dangers in using criteria such as 'striding' and 'propulsive' bipedalism, even tacitly, as diagnostic criteria. For instance because of the apparent locomotor compatibility of the tibia and fibula from the FLK site at Olduvai Gorge (at present OH 35) and the foot, OH 8 from FLKNN, it has been suggested that OH 35 is more likely to be associated with the second individual on the FLK floor, OH 6, than with the better known cranium OH 5 (M. D. Leakey, 1971). Similarly when the affinities of OH 10 were being considered it was stated that "a comparable type of gait has already been ascribed to the *Homo habilis* foot ----" (Day & Napier, 1966); this has led subsequent investigators to treat OH 10 and OH 8 as parts of the same functional foot complex (Preuschoft, 1971).

Now that new material is available, and its study under way, the post-cranial material from Olduvai, and OH 8 and OH 10 in particular, occupy a critical position for a number of reasons. First, the functional labels that have been applied to specimens, *Homo habilis* and otherwise, may influence judgements about new material. Second, material that has been attributed to *Homo* may in fact belong to any of the other taxa that are represented at Olduvai. Third, re-examination, with the great benefits of hindsight, may show that locomotor inferences about this material may need modification, especially if it is accepted that different hominid bipedal morphotypes may have been evolving in parallel in the Plio-pleistocene.

OH 8

This is a collection of adult left foot bones; they articulate with each other and there is no doubt that they represent a single individual. It was found in Bed I at site FLKNN in 1960 during the course of excavations. It lay on an occupation floor and evidence of erosion and scavenger activity indicates that the floor was a relatively open system (M. D. Leakey, 1971). Two proximal phalanges are catalogued under the same number. Specimens found *in situ* on the same occupation floor are OH 7 (L. S. B. Leakey, 1961), two metatarsals (OH 43), a clavicle (OH 48) and part of the shaft of a radius (OH 49): other material has been found on the surface and on an erosion slope beneath the site. There is therefore evidence of at least two individuals on this floor and there is no reason to associate this adult foot with OH 7, the juvenile type specimen of *Homo habilis*. The left metatarsal bones (OH 43) represent a second adult individual on the floor. This horizon lies only a few feet below the level of the 'Zinjanthropus' floor at site FLK, some 300 yards away; the probable age for the OH 8 foot is 1.7 million years (Hay, 1971).

The foot was described by Day & Napier (1964). They concluded, on the basis of many features, that the foot possessed the requirements for a "fully bipedal gait", but added the caveat that it may not have been "precisely parallel to that of modern man". Probably on the basis of these conclusions OH 8 was included as a paratype into *Homo habilis* and features of it are cited as characters of that species, (L. S. B. Leakey, Tobias & Napier, 1964).

Further studies were made on the talus. Lisowski (1967) dissented from the views of Day & Napier and suggested that the foot was "far more like that of living monkeys and apes than that of man". An anatomical examination of the talus, linked with a multivariate analysis, led Day & Wood (1968) to confirm Day and Napier's findings and to write "while OH 8 is the foot of a biped, the striding bipedal gait of man had not been achieved". The results of the multivariate analysis showed the Olduvai talus to be unique when compared with those Primate locomotor groups examined, but quite similar to the fossil talus from Kromdraai.

A biomechanical analysis of the foot (Preuschoft, 1971), concluded that it was "unlikely to be a prehensile foot", and that features such as the significant angle of dip of the neck could be interpreted as adaptations to reduce bending stresses in a bipedal gait. A comparative anatomical study of the hallucial tarso-metatarsal joint in Primates indicated that the features of that joint in the OH 8 foot are "strikingly conservative" and that the Olduvai foot "still bears some of the hallmarks of transition from arboreal to terrestrial life" (Lewis, 1972). Archibald, Lovejoy & Heiple (1972) showed that the metatarsal robusticity formula in OH 8 was unusual, but present, in a sample of modern men.

Thus, while there are good anatomical and biomechanical grounds for rejecting this as a prehensile foot, it is not a necessary corollary that it is therefore directly related to the modern human morphological pattern. Day & Napier (1964) wisely stated that the features they listed as the adaptations of modern Man were specific for the modern human morphotype and gait pattern. The partial or total expression of these features in a fossil foot is *a posteriori* no guarantee that the fossil represents a developmental stage towards the modern human morphotype or gait pattern. Equally well a fossil foot may have been bipedal and not have these, but another combination of characters. In the context of talar morphology examples of similarly misleading features are the angle of torsion and the horizontal angle of the neck. The high angle of torsion in Man (presumably because of the low values in apes) has been correlated with "the human type of gait" (Lisowski, 1967); in fact *Colobus* and other monkeys have a comparable mean

Table 1 Data for modern Man and the fossils. Details of the modern human sample are given in Day & Wood (1968)

Variables	Modern Man		OH 8	Kromdraai KNM-ER813	
	Mean	s.d.			
Horizontal angle	19.0	3.4	28.0	32.0	14.0
Dip angle	35.9	4.9	8.0	4.0	25.5
Torsion angle	37.0	7.2	40.0	34.0	48.0
Neck length ind.	135.0	18.0	125.0	121.0	130.0
Head proj. ind.	42.0	10.6	45.0	72.2	40.0
Troch. shape ind.	93.0	8.3	100.0	106.0	91.0
Fib. facet proj. ind.	284.0	63.0	333.0	360.0	222.0

torsion angle. It was also accepted by some (Straus, 1963), that a wide horizontal angle went *pari passu* with an abducted hallux; the OH 8 foot demonstrates that this is not necessarily so.

These examples indicate that unless characters have been investigated as part of a comprehensive comparative and biomechanical study their valency as special functional indicators must remain suspect. Perhaps it would be more prudent to say of such features as a low longitudinal arch, a relatively horizontal subtalar joint, an adducted hallux, the tarso-metatarsal joint and the pattern of metatarsal robusticity in the Olduvai foot that, taken together, they strongly suggest a definite bipedal capability.

New evidence from East Rudolf may also be relevant. A talus, KNM-ER813, found in 1971, was considered on preliminary examination to belong to *Homo* (R. E. F. Leakey, 1972). More detailed anatomical examination added nothing to alter this attribution (R. E. F. Leakey & Wood, 1973). Comparison with the tali from Kromdraai and Olduvai revealed many differences between them and KNM-ER813; these are summarized in the measurements given in Table 1. The results of submission of these data to the types of multivariate analysis used by Day & Wood (1968, 1969) confirm that KNM-ER813 is very similar to two groups of modern human tali (Wood, 1974); the results of the D^2 distance analysis are given in Table 2. While individual features are open to misinterpretation, the several variables used in this analysis, and the nature of the multivariate technique itself, make it most likely that the degree of similarity of overall morphology as expressed in the D^2 results is a valid indicator of genetic and functional affinities. Thus, broadly contemporary with OH 8, is a talus that has a better claim to belong to a *Homo* foot. If the present taxonomic scheme is accepted an anomaly exists as the talar

Table 2

Mahalanobis D^2 distances and probability levels between groups and special cases

Fossils	Comparative Groups				
	1. <i>Homo</i> Dissecting room	2. <i>Homo</i> Anglo Saxon	3. <i>Homo</i> Bushmen	4. <i>Gorilla</i>	5. <i>Pan</i>
KNM-ER813	15.9 (2.5-5%)	24.2 (0.5%)	12.0 (5-10%)	47.3 (<0.1%)	48.1 (<0.1%)
Olduvai	66.1 (<0.1%)	70.2 (<0.1%)	49.8 (<0.1%)	57.5 (<0.1%)	43.5 (<0.1%)
Kromdraai	84.9 (<0.1%)	89.5 (<0.1%)	65.6 (<0.1%)	63.0 (<0.1%)	51.9 (<0.1%)

morphology of the two *Homo* specimens is very different. To postulate such wide variability of a key structure in one lineage is to introduce unacceptable complications into hominid phylogeny; a better solution would be to place these specimens in different taxa. When these new data are added to the fact that OH 8 is similar in some ways to the Kromdraai talus, it is a reasonable suggestion to attribute OH 8 to the genus *Australopithecus*.

OH 10

This is the distal phalanx of a right hominid hallux. It was found in Bed I at site FLKN on the occupation floor at level 5 (M. D. Leakey, 1971). No other hominids were found *in situ* but an isolated hominid tooth (OH 21) was found on the surface (M. D. Leakey, 1969). This phalanx is broadly contemporary with OH 8.

It was reported on by Day & Napier (1966). They noted that although it most strongly resembled the bones of modern men "its morphology is not precisely matched by any of the hominoid bones or casts that have been examined". Two features were considered to be particularly relevant. These were valgus deviation, which is most conspicuous in modern Man, and axial torsion, seen in modern Man and not in the extant African apes. The expression of these characters in OH 10 led the authors to suggest that "the Olduvai toe bone belonged to an upright bipedal hominid possessing a plantigrade propulsive gait". In a multivariate study Day (1967) wrote of the results that they implied that "propulsive bipedalism, of the human type, was the form of gait of at least one group of early hominids evolving in East Africa at this time"; this was in reference to OH 10. The only other study to include the bone is that of Preuschoft (1971) who concluded that this form "obviously had no prehensile foot". The claims made for the locomotor pattern of the hominid, whose hallucial phalanx this was, are definite and specific but they should nevertheless be examined critically.

It was the findings of Wilkinson (1954) that prompted Barnett (1962) to investigate the valgus deviation of the terminal hallucial phalanx. He found no such deviation in 164 non-human Primates and he therefore suggested that the presence of valgus deviation in a fossil form would "provide evidence for a human type of gait". However, just because a particular form of bipedalism is associated with a morphological feature, the presence of that feature need not imply the same pattern of locomotion; it is the classical *post hoc* fallacy. Barnett recognized this, for in the same paragraph he wrote "examination of many members of all the principal primate species would be necessary before this distinction can be regarded as absolute". It may subsequently be demonstrated that Barnett's suggestion is correct, but his findings are not evidence alone, and he recognized

this. At any event, the deviation of the OH 10 specimen apparently lies within 2 standard deviations of gorilla and outside the same range for modern Man (Day & Napier, 1966). The data on axial torsion are more impressive but, until sufficient comparative studies have been undertaken, are open to the same logical objection.

The results of the multivariate analysis (Day, 1967), might have resolved this issue. In this study, the weights of the first canonical variate acted as a successful discriminant between the hallucial terminal phalanges of modern Man and the African apes. The same weightings applied to the fossil data grouped it with the modern men. This would be most significant if the D^2 distances between the fossil and the modern human groups were small and insignificant. However, Figure 2 in Day (1967) and Table 3 below, show

Table 3 D^2 distances (taken from Day, 1967) and probability levels between groups and OH 10

Fossil	Comparative Groups				
	1. Modern Man (European)	2. Modern Man (East African)	3. Modern Man (Bushmen)	4. Gorilla	5. Pan
OH 10	29.0 <0.1%	32.8 <0.1%	26.5 <0.1%	62.9 <0.1%	66.7 <0.1%

that though the fossil is further from the apes than from the men it is still a significant distance from the men. Oxnard (1972) has pointed out recently how this situation can give rise to misleading canonical analysis results; a reanalysis of data from Miocene tali (Wood, 1973), has revealed a similar case. Unless it can be demonstrated that this toe bone analysis was not subject to the same potential error the results must be reinterpreted as being no more than equivocal about the specifically human bipedal capabilities of this phalanx.

These comments may perhaps be justly criticised for being pedantic and ignoring the practical difficulties of dealing with an inadequate fossil sample. Indeed most of the locomotor inferences were only suggestions, but even suggestions have a way of becoming incorporated into hominid 'folk-lore' in the guise of proven facts. When more data are available these locomotor predictions may be vindicated, but meanwhile the evidence for them is equivocal. While this is so, it is important that specific functional epithets should not be attached to *Homo habilis*. For, not only may they be incorrect, but the specimens on which they were based may not even belong to the genus *Homo*.

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The Age and Stratigraphic Position of Olduvai Hominid I

A short history of Olduvai Hominid I is given. On the basis of absolute and relative dating its position in the Naisiusiu Bed, part of the former Bed V, is affirmed. Some connection, on morphological grounds, with other hominids in East Africa is postulated, as well as with cultural material.

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1. Introduction and Discussion

This famous site in Tanzania was first discovered and named Olduvai (German-Oldoway) in 1911 by Professor Kattwinkel of the Bayerische Palaeontologische Staatssammlung of Munich. Then, in 1913, the institution conducted the "Zentralafrikanische Expedition" in conjunction with the Geological and Palaeontological Institute and Museum of the University of Berlin. In order to obtain geomorphological and other scientific information, a three month trial excavation was undertaken at the Gorge. A preliminary report (Reck, 1914) dealt with the archaeological, anthropological and palaeontological finds; the Olduvai Hominid I, the first of the numerous hominids later found, was first mentioned in this report. Reck (1914) made a preliminary division of the stratigraphy of the gorge into five levels. During the excavation of a trial trench, the second lowest stratum yielded the human skeleton. It was found on the sloping surface of Bed II, 3–4 m below the top of the gorge, which shows a maximum depth of *c.* 50 m at this locality. The skeleton, which was in near perfect condition, was divided into skull and postcranial remains, and these were transported separately to Berlin.

The contracted position of the individual suggested the possibility of a burial. Reck denied this at first, but later it was proved to be correct. No cultural material was found in association with the skeleton or in the immediate vicinity. Consequently, the excavator suggested that the individual had actually drowned in a lake that was present during that time. He dismissed any other possibility of deposition of the individual since he reported that the find came from the homogeneous deposit of Bed II and not from the sloping surface. The skeleton thus belongs to the "normal, undisturbed, somewhat clayey-tuff" (Reck, 1914), and all evidence points to the indigenous position of the skeleton in the stratum in which it was found.

Several relative-dating-indicators, such as the associated extinct fauna and geologic-tectonic-stratigraphic location of the stratum itself, indicated the possibility of a very old age for the skeleton. It was thought that the skeleton could be of pre-pluvial times. The thickness of layers above the skeleton itself also indicated the long time span necessary for the deposition of such strata. Geologic as well as palaeontologic facts seemed to show clearly that the "skeleton-horizon"—and thus presumably the skeleton itself—could not be of recent times and that both belonged to a time during which a pluvial in Africa was prevalent. Reck (1926) revived the argument of the age of the hominid twelve years

later and concluded that modern Man existed at a very early time, specifically in East Africa. Leakey, who had continued work at Olduvai after Reck, wrote a short report (1928) dealing with the morphology of the skull of the hominid and agreed with previous investigators by ascribing it to *Homo sapiens*.

The first thorough morphological investigation of the find occurred 16 years after its discovery. Gieseler & Mollison (1929) provided a detailed description of the site, location of the skeleton, morphology of the postcranial skeleton, state of fossilization of the bones, and morphological description of the skull. Between 1913 and 1929 it had become popular to speculate about the chronological position of the hominid remains so the reevaluation of the material was badly needed. Closely following Reck's original report, Gieseler assumed that the skeleton came from horizon 2 (Bed II), but at the same time he asked whether burial or intrusion at a later time might be possible. Mollison stated that the individual was definitely buried. Reck had indicated that even though the individual was found in a flexed position, it probably was not an intended burial, but a natural position at the time of death. Some specialists had claimed that the contracted position indicated that parts of the body were bound after death, probably a fairly recent custom in the history of mankind. Gieseler's opinion, based on the state of fossilization of the bones, seemed to support Reck's view that the skeleton was of considerable age. The morphology of the postcranial skeleton suggested that the individual belonged to *Homo sapiens*. This evaluation was primarily based on the physical differentiation of the morphological features and appearance of the long bones as compared to other fossil hominids, such as *Homo neanderthalensis* (*Homo primigenius*), according to the method given by Klaatsch (1901). By taking measurements according to the Manouvrier—tables, using radius and ulna, the size of the individual was estimated to be between 180.3, and 181.2 cm. This size would correspond roughly to the average size of present-day Masai living in this area.

Mollison tried to get some idea about the relative age of the individual by devising a measurement of the organic content of the bones, using ultraviolet fluorescence. His percentage of the organic content of the Olduvai hominid was 4.8. In order to have some comparison to other hominid remains, Mollison applied the same method to hominid bones from the Ofnet-Cave in Bavaria. The assumed age of the latter was Azilian, even though no cultural material was associated with the skulls. Since his measurements on an Ofnet-skull came to 5.3% he decided that the Olduvai individual was somewhat older and he placed it in a time period equal to the final stage of the European Magdalenian. Mollison assumed that the decrease in organic content in bone was a simple function of time, disregarding environmental influences. Measurements by microanalysis and computation of the organic content (collagen) by this investigator proved to be drastically different from Mollison's results. The Ofnet material has an organic content of 16.56% which is three times as large as that calculated by Mollison, whereas Olduvai Hominid I has only 2.70%. The difference in absolute age of the Ofnet-hominids and Olduvai H1 of c. 4000 years has no relationship to the percentage difference in organic content between these two hominids. The radiocarbon age of the Ofnet-hominid is $13,100 \pm 100$ years (UCLA-1783) (Glowatzki & Protsch, 1973). Mollison's usage of ultraviolet fluorescence to estimate the organic content was one of the first attempts to get some idea of a relative age on bones but the method later proved invalid. He obtained identical results for the organic content of the hominid and the fauna of Bed II, but in fact, both are far apart in time. Experiments were also





conducted on measuring the difference in porosity of the bones as a possible indication of relative age. If different porosity, and therefore different states of fossilization, was an indication of age, then the fauna were relatively older.

The skull belongs to a male of fairly advanced age, well over 40 years. This evaluation is based on the complete closure of certain sutures, such as the sagittal and coronal, as well as partial obliteration of the lamboid suture. This morphological evaluation is in agreement with Mollison's description (1929). The specific tendency of obliteration of the nasal suture as it occurs in high percentages in Negroids, Hottentots and Bushmen is not evident here. Many investigators concerned themselves with the apparent hyperdolichocephaly of the skull with a cranial index of 66. It should be emphasized that most of this hyperdolichocephaly is probably due to post mortem distortion. This distortion is also somewhat evident on the elliptical foramen magnum. The individual lay on his right side; the left side, mainly the parietal, was severely damaged. The right parietal, frontal, and occipal bones are also cracked in several places. The total appearance of the skull is, as Mollison pointed out, of a somewhat "cocoon form" appearance (1929). Most of the deformation probably occurred when the bones were still fresh, shortly after burial, until they eventually cracked. The tuber parietale is thus quite pronounced due to this post mortem deformation. Other post mortem deformation effects can be seen in the extreme hyperleptoprosopy (facial index of 102), orbital index of 90, and the extreme height of maxilla and mandible. With most of the left side being severely damaged, reconstruction can only be hypothetical, probably leading to a high cranial index. Therefore, most of the morphological peculiarities should not be taken as physical characteristics of the living individual, but as post mortem deformation effects. Some of the above deformations were also noticed by Weinert and Fischer (Weinert, 1934).

The controversy over the age of the skeleton was revived in the early 1930's by several investigators. Many of them could not believe that *Homo sapiens* existed at such an ancient time as the geological period in which Bed II was formed. Boswell (1932) suggested a more careful investigation of the geological deposits directly associated with the skeleton itself. Solomon subsequently started a petrological investigation of a sample of earth from within the skeleton. He found at least one mineral, amphibole, which was absent from Beds II and III. This mineral was present in Bed IV. Chips of concretionary limestone which are indistinguishable from that of Bed V were also found in the earth. Thus he concluded that the skeleton was contemporaneous with Bed V (post-Aurignacian).

In the same year, August 1932, Hopwood (1932) presented arguments for the possible contemporaneity of the hominid and Bed II, but his only proof was the original stratigraphic reports of Reck. The uncertainty of the relative age of the skeleton was finally solved when Leakey *et al.* (1933) agreed, after careful consideration of all facts, that the skeleton must be intrusive into Bed II and that the date of intrusion was not earlier than the great unconformity which separates Bed V from the lower series of beds. It seems certain that the skeleton was deposited where it was found before the main portion of Bed V and the overlying steppe-lime was formed (Leakey *et al.*, 1933). The skeleton seems to have been buried at the base of Bed V. This relative chronological estimation seems to be strengthened by the cultural material, Upper Kenya Capsian C, which was also found in other places at the base of Bed V. This culture is approximately equal in time to the same cultural assemblage found at Gamble's Cave (Gamble's Cave II) and associated with similar physical types buried in contracted position.

Even though some specialists still adhered to the view of an early age of the hominid skeleton (Dietrich, 1933), most others argued in favour of the recency of the remains (Weinert, 1934). Weinert argued against an early age of these *Homo sapiens* remains from a purely theoretical evolutionary point of view. He could not believe in the sympatric existence of *Homo sapiens* and *Homo neanderthalensis* on a subspecies or racial level. And what if *Homo sapiens*, as some suggested in the case of the Olduvai hominid, is even older than *Homo neanderthalensis*? From all evidence available, Weinert concluded that Olduvai Hominid I was a surface find and quite recent, thus eliminating him as one of the earliest *Homo sapiens* specimens. Reck had reported Olduvai Hominid I in Bed II, whereas it should have been pictured more properly on top of the sloping surface of Bed II, on the edge of the gorge. Because of erosional processes no one will ever be able to tell how deeply the skeleton was originally covered by earth before redeposition. This is exactly one of the questions which can be solved with absolute dating; the stratigraphic position and association with other materials of the skeleton.

Theoretically, several facts speak against an early age of the hominid, such as its morphology and its possible association with Bed V. Also a relative age determined by the state of fossilization of bones is invalid for a positive chronological diagnosis. Leakey (1935) repeated and elaborated on his and other specialists' earlier position (Leakey *et al.*, 1933) and added that the possible relative age of the now Bed V hominid could be equated in time to the Gamble's Cave hominid remains associated with an Upper Kenya Capsian C. The contemporaneity was not based on association of the hominids in both localities with that culture, but on the association of one with that culture and similar physical types of the hominids in both sites. The subsequent agreement of specialists was that in relative time the skeleton was younger than Bed IV, probably contemporary with Upper Kenya Capsian C (Boule & Vallois, 1957; Ivanova, 1972).

2. Present Archaeological and Chronological Interpretation

Extensive work was conducted in recent years on the stratigraphy of Olduvai Gorge, resulting in more specific evaluation and renaming of the upper strata. L. S. B. Leakey (1967) divided the upper portion of the gorge into Bed Va, Bed V, the steppe-limestone, and Bed VI. However, no absolute dates were available on any of the beds above Bed IV until 1968 (Leakey, Protsch and Berger, 1968). A sample was processed which consisted of faunal bone taken from the fawn-coloured aeolian deposit of Bed V on the northern side of the gorge, where it is cut obliquely by the fifth fault. Bed V was approximately 4.60 m thick at this part and had eroded to some extent, a circumstance facilitating the collection of bone samples. This radiocarbon date established the upper limit of the later Upper Kenya Capsian at $10,400 \pm 600$ (UCLA-1321).

The stratigraphy of the upper levels of Olduvai Gorge was again revised in 1972. In a publication dealing with the dating, cultural assemblages, and geology of the former Bed V, new names and subdivisions were proposed by Leakey *et al.* (1972). The sections of the uppermost sequence, previously termed Bed V and Bed Va, were found to overlap extensively in age and were thus abandoned as vertical stratigraphic subdivisions. The upper part of the sequence was subdivided into a younger formation, the Naisiusiu Bed, and an older formation, the Ndutu Bed. On the north side of the gorge, 110 m west of the second fault, the Naisiusiu Bed is made up of three units: a basal unit of stream

sediments, a middle unit of sheet wash deposits, and an upper unit of aeolian tuffs. The middle section of the Naisiusiu Bed, the sheetwash deposits, contains abundant microlithic tools (Leakey *et al.*, 1972). In 1969 samples of ostrich egg-shell and faunal bones were collected for radiocarbon dating from the middle unit. The previous date on the upper portion of the Naisiusiu Bed of $10,400 \pm 600$ BP (UCLA-1321) and the new dates for the middle portion of the Naisiusiu Beds of 17,000 BP (Lamont) and $17,550 \pm 1000$ (UCLA-1695) give accurate uppermost Pleistocene dates for this large upper portion of the Naisiusiu Bed. This suggests a total time span of about 30,000 years for the total Naisiusiu Bed. The industries described from the upper portion of former Bed V were regarded as Upper Kenya Capsian, but the new microlithic assemblage from the middle unit of the Naisiusiu Bed differs in certain respects from the Upper Kenya Capsian. The bones used for dating were very fragmentary, but were probably those of Equidae and possibly also Bovidae. Most of the microlithic tools were found 17 to 23 cm below the horizon of bone concentration. The industry is different from the Upper Capsian in that a number of Capsian tool types are lacking; some of the dissimilarity might also be due to different raw materials used. Those tools which are common to both industries do not correspond at all closely in frequency and thus make them quite different from Upper Kenya Capsian sites like Gamble's Cave II and the Naivasha Railroad Rock shelter. The industry does not yet have an exact parallel anywhere, and it may represent a local variant of the Kenya Capsian. It is less specialized and may prove to be an early form of Wilton not yet recorded in this area.

3. New Chronological Interpretation

With the new absolute dates on the former Bed V the question of the chronological position of the Olduvai Hominid I still remains. Was he really contemporary with the Gamble's Cave II individuals and Upper Kenya Capsian C, since he was a similar physical type, or was he possibly the maker of the chronologically earlier industry of the middle unit of the Naisiusiu Bed? Since the cranial material was too valuable to be used for dating, it was decided to process only postcranial material. However, even though the total skeleton is catalogued in Munich, only the skull itself could be found in "Anthropologische Staatssammlung". Evidently, most of the postcranial skeleton had disappeared by the end of World War II.

Through the courtesy of G. Glowatzki, director of the Staatssammlung, some very fragmentary postcranial material still imbedded in earth was found and used for radiocarbon dating. This material consisted mainly of rib fragments, long bone fragments, and some pieces of vertebrae. Some of the bones were covered by the preservative Sapon, a lacquer, which was easily flaked off and removed. Many parts were not covered with this preservative, but nevertheless the same chemical pretreatment was given to all bone material. After preliminary cleaning, a total amount of 224 g of bone was available for dating. This postcranial material most likely belongs to the Olduvai Hominid I since it was marked as such. However, to check whether the skull and the fragmentary bones belonged together, two separate microanalytical tests were made on the skull and some post cranial primary bone. The values of 0.45% (British Museum) and 0.43% (UCLA) are remarkably similar and give support to a positive association of the bones (Table 1).

Since only one test could be taken on uranium, no suggestion can be made as to a relative placement in time based on this element. One could argue that a comparison of microanalytical results of nitrogen and uranium between the fauna from the middle unit of the

Table 1

Microanalytical results of Olduvai

Laboratory number	Material	Bed	U(p.p.m.)	F(%)	N(%)
UCLA-1740	Bone, Hominid	Middle Naisiusiu	3	—	0.45
B/M-HJW/184-6957	Bone, Hominid	Middle Naisiusiu	—	—	0.43
UCLA-1695	Bone, Fauna	Middle Naisiusiu	3	—	0.64
UCLA-1321	Bone, Fauna	Upper Naisiusiu	2.5	1.1	1.21

Radiocarbon dates of Olduvai

Laboratory number	Material	Stratum	Age (Years BP)
UCLA-1321	Bone, Fauna	Uppermost Naisiusiu	10,400 $\pm$ 600
Lamont?	Ostrich Shell	Middle Part Naisiusiu	17,000 $\pm$?
UCLA-1695	Bone, Fauna	Middle Part Naisiusiu	17,550 $\pm$ 1000
UCLA-1740	Bone, Hominid	Middle Part Naisiusiu	16,920 $\pm$ 920

Several other radiocarbon dates were run, but could be contaminated by either recent or old radiocarbon, since these sample materials were mostly calcrete or fresh water shells.

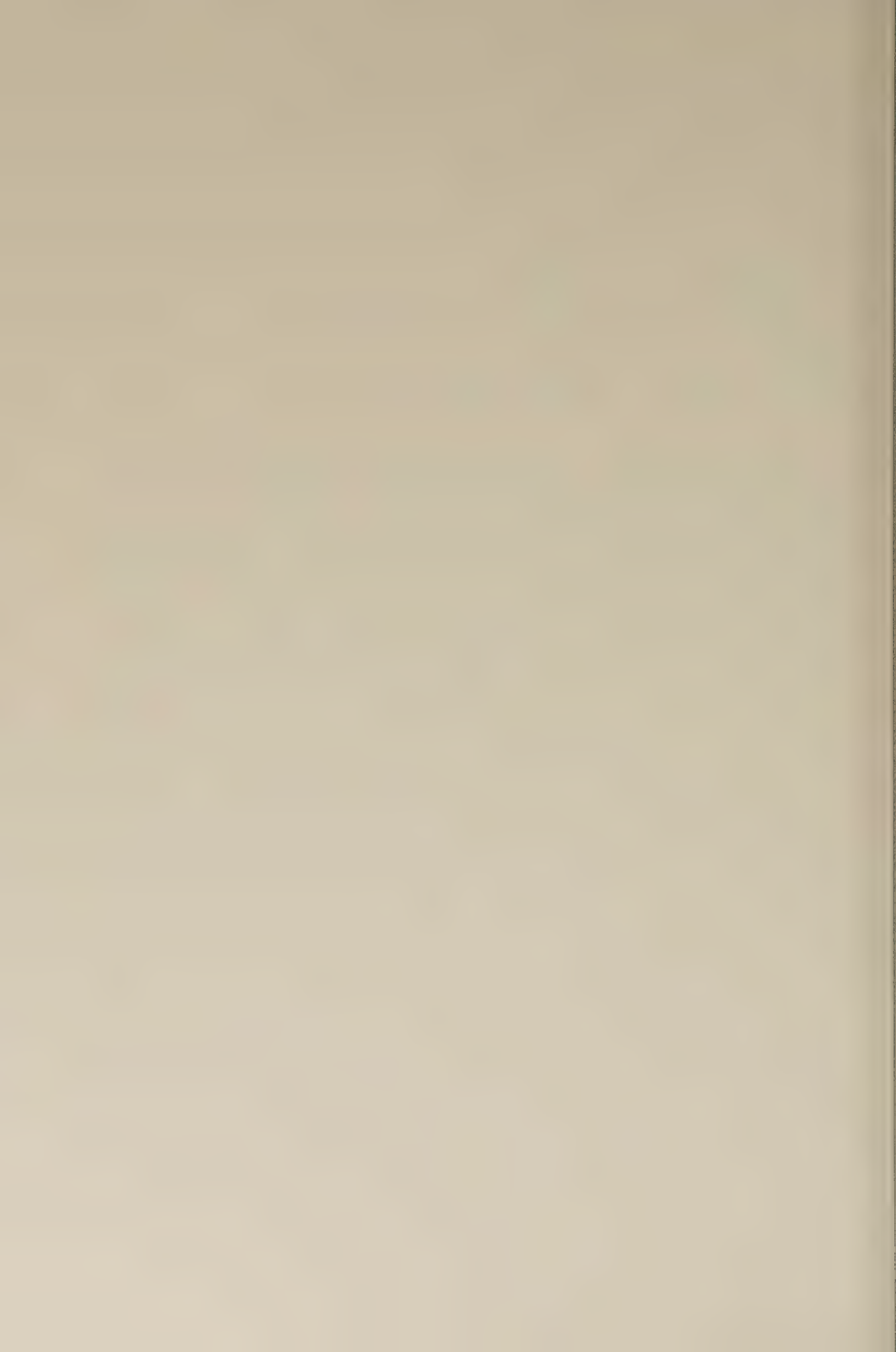
Naisiusiu Bed (UCLA-1695) and the Olduvai Hominid I (UCLA-1740) could verify their contemporaneity in relative age. The results of both samples are indeed similar, but they do not allow a valid conclusion as to relative age placement, since one of the samples was probably subjected to surface exposure. Furthermore, both samples originated from different localities, and were thus subjected to different microenvironmental conditions in the Bed itself. The results on the organic content of the bones taken by UCLA and the British Museum are in disagreement with the results by Mollison in 1929. Since only 224 g of bone were available for dating, only 32.23% of the counter could be filled. The age of UCLA-1740 came to 16,920 $\pm$ 200 years. This date can be interpreted in several ways. The individual, Olduvai Hominid I, dates to the middle unit of the Naisiusiu Bed, contemporary with the microlithic industries dated to approximately 17,000 years. The individual does not date the final period of the former Bed V, contemporary with the Gamble's Cave II individuals and the Naivasha Railroad Rockshelter individual. Since the latter two sites have dates of *c.* 8200 and 10,600 on skeletons displaying similar morphological characteristics as Olduvai I, it can be assumed that the same physical type existed in this area for at least 9000 years. This individual from the Olduvai Naisiusiu Bed also displays some morphological characteristics similar to the contemporary Lukenya Hill individual (Gramley, Gramley & G. P. Rightmire, 1973).

There seems to be some indication that the cultural remains associated with Lukenya Hill man are somewhat unusual and earlier than the Upper Kenya Capsian. It remains to be seen in the latter site what the ultimate cultural evaluation of the industry associated with the human remains will be.

Contrary to Leakey *et al.* (1933), Olduvai Hominid I was not buried at the base of Bed V (Naisiusiu Bed), but in the middle portion of that bed. It represents morphologically a similar physical stock as Gamble's Cave II, Naivasha, Lukenya Hill, and might have persisted in this area for at least 9000 to 10,000 years. It was probably the maker of the "Proto-Wilton?" culture found in the middle unit of the Naisiusiu Bed. I propose to refer to the former Bed V hominid, Olduvai Hominid I, also as the Naisiusiu hominid.

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Reiner Protsch

*Fachbereich Biologie—Anthropologie,
J. W. Goethe Universität,
Frankfurt a.M.,
West Germany*

Hertha de Villiers

*Department of Anatomy,
University of Witwatersrand,
Johannesburg, South Africa*

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Absolute dating of several stratigraphic levels position an infant's mandible relatively to about 29,500 years ago. This mandible may represent the infant stage of an early Negroid form of *Homo sapiens afer* and was probably associated with cultural material belonging to the transition of the Middle Stone Age to the Late Stone Age.

1. Chronology

The first extensive report on the Bushman Rock Shelter appeared in 1969 by Louw, Brain, Vogel, Mason & Eloff. This rock shelter is located in the Eastern Transvaal of South Africa near Origstad. It was known for several years prior to 1965 that the shelter contained prehistoric material; at that time the owner, J. D. Claassens, called it to the attention of scientists at the University of Witwatersrand in Johannesburg.

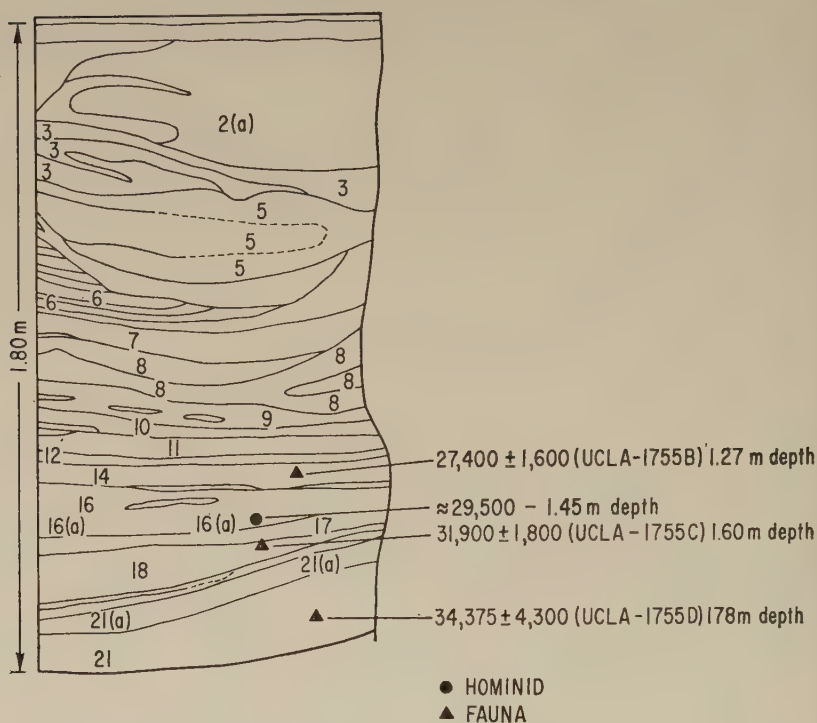
Stimulated by the finds of a preliminary investigation by J. J. Malan and R. J. Mason who had collected some Middle Stone Age implements at the shelter, A. W. Louw started a two week trial excavation during June and July of 1965. He began excavation in the back of the rock shelter, which at its maximum is 50 m wide and measures about 19 m from the back rock wall to the edge of the talus in front of the shelter. The deposit was disturbed: several years ago a farmer dug a huge hole in the mid-section of the shelter. There are two smaller holes in the rear of the shelter which he probably dug at the same time. They are now located on each side of the trial trench.

Stratigraphically the layers were numbered from 1 to 43. The cultural material found in these layers consisted of Iron Age industries in Layers 1 and 2, Later Stone Age industries in Layers 3 to 27, and Middle Stone Age industries in Layers 28 to 43. Each of these layers contained abundant organic materials for dating purposes. Faunal remains appeared throughout the total stratigraphy, some charcoal and wood were present down to Layer 18 and were also in the topmost Middle Stone Age layer, Layer 28. Whereas the cultural material of Later Stone Age affinity in Layers 3 to 27 was sparse, artifacts belonging to the Middle Stone Age were more numerous in Layers 28 to 43. The Bushman Rock Shelter was also the first rock shelter or cave in the Eastern Transvaal which contained cultural material belonging to the Middle Stone Age.

Louw had not reached bedrock during his excavation in 1965, and a second excavator, J. F. Eloff decided in 1967, to start new excavations in an area adjacent of Louw's trial excavation in the rear of the shelter. Eloff has presently excavated down to a depth of approximately 25 cm below the depth reached by Louw in 1965. The lowest layers of the stratigraphy, the Middle Stone Age material, showed some resemblance to the Earlier Pietersburg artifacts of the Cave of Hearths Bed 4. Some layers also seemed to indicate a transitional phase from the Middle Stone Age to the Later Stone Age (Eloff, 1969: 60).

Eloff's excavation brought forth abundant faunal materials and fragmentary portions

Figure. 1. Stratigraphy of Bushman Rock Shelter.



of the material were used for radiocarbon dating at UCLA. Prior to these bone dates, nine radiocarbon dates were processed by J. C. Vogel at Groningen, mainly using organic materials such as charcoal and wood with the exception of one date on charred bone. All these materials came from Louw's 1965 excavation. Four of these samples dated the Middle Stone Age from greater than 53,000 years ago to 12,090 years ago. Three samples dated the Later Stone Age from 12,160 years to 9570 years. Whereas one sample with 9940 years indicated a mixture of Middle Stone Age and Later Stone Age materials, another one of 12,470 years was not apparently associated with any cultural materials (Table 2).

Mason (1969) explained the recency of dates such as GrN-4816 ($12,510 \pm 105$) in a Middle Stone Age layer by proposing that Later Stone Age occupants of the shelter walked on and disturbed the surface of the Middle Stone Age gravel, Layer 28, thus adding the wood to an earlier layer, as well as churning up Middle Stone Age tools found in Layer 27. Looking at these charcoal dates it seems that the Later Stone Age occupation began in Layer 27 at around 12,510 years ago. Too little is known, however, about peculiarities of deposition and disturbances in caves and rock shelters. The recent date of the above radiocarbon measurements could also be explained by growth of roots of more recent plants into lower layers, thereby introducing materials yielding much more recent absolute dates.

Further absolute dating of the stratigraphic portion which Eloff excavated seemed to be desirable. In order to avoid dating of possibly intrusive materials such as plant roots, the new dates specifically concentrated on bone materials. These dates would then in turn give a fairly accurate date for hominid remains found in any level or layer of the shelter,

as well give a good date to the transitional phase from Middle to Later Stone Age industries.

Collection of the bone material used for radiocarbon dating of several layers of Bushman Rock Shelter was mainly undertaken in order to obtain a date for an infant hominid mandible found in 1969 by a tourist guide, a Mr van Zyl. The infant mandible was handed to Dr J. D. Claassens, owner of the farm on which the Bushman Rock Shelter is situated, who then presented the mandible to Professor J. F. Eloff in 1970. According to Mr van Zyl the mandible was protruding partially from the wall of the excavation apparently between Layers 14 and 18. The morphological description of this mandible follows at the end of this section. The "nonfossilized" fresh appearance of this mandible made specialists doubt its association with a stratigraphic location between Layers 14 to 18. It should be pointed out that in Eloff's stratigraphy, Level 18 is approximately representative of the transition between Middle Stone Age to Later Stone Age cultural materials, whereas Louw designated this transition to approximately Layer 27 to Layer 28. If this mandible came from Level 18 or a slightly more recent level, it would be representative of an individual from an earlier Later Stone Age industry.

It should be pointed out that the physical appearance of bones does not permit an accurate judgement as to the placement of bones in time. Microenvironmental differences can change the appearance of bones dating to the same time period. Therefore, it was decided to measure several bone samples from Levels 14, 18 and 21 by microanalysis and radiocarbon. This could also provide a date for the hominid mandible in that stratigraphy.

Three fragmentary bone samples were chosen from Levels 14, 18 and 21 and the burned bone material sorted out. Microanalysis concentrated on nitrogen and uranium via radon. Expected decreasing values in the nitrogen readings were evident from Levels 14 to 21 with concomitant increasing values in uranium from Levels 14 to 21. This regularity in the data indicates lack of disturbance of the deposit in this section of the cave. The nitrogen reading of the hominid mandible could be representative of a stratigraphic location of that mandible between Levels 14 and 18, more specifically Levels 16 or 17 (Table 1).

After sorting out the burned bone material, several hundred grams of bone were available for three radiocarbon dates. These were processed by a refined method of collagen-radiocarbon dating as described by Berger, Protsch, Rozaire & Sackett (1971),

Table 1 **Sample weight of Bushman Rock Shelter**

Laboratory number	Material	Location	Weight (g)
UCLA-1755B	Faunal Bones	Level 14	317
UCLA-1755C	Faunal Bones	Level 18	424
UCLA-1755D	Faunal Bones	Level 21	336

Microanalytical data of Bushman Rock Shelter

Laboratory number	Material	Level	U p.p.m.	N(%)
UCLA-1755B	Fauna	14	6	0.93
UCLA-1755F	Hominid	16/17	—	0.86
UCLA-1755C	Fauna	18	9.5	0.69
UCLA-1755D	Fauna	21	12.5	0.64

Protsch (1970, 1972, 1973) and Protsch & Berger (1973). Since the nitrogen concentration of each sample was above 0.5 %, enough organic carbon was available to fill the 7.5 l. gas proportional counter to its capacity. Contrary to expectations, only 52.95 % of the 7.5 l. CO₂ proportional counter was available from sample UCLA-1755D from Level 21. It dated to $34,375 \pm 3800$ years. Even though the counting time of this sample was increased, the error is still fairly large. Sample UCLA-1755C dated Level 18 and yielded a full counter of CO₂ with an age of $31,900 \pm 1800$ years BP. Sample UCLA-1755B from Level 14 yielded only 55.49 % of the volume of the counter and had an age of $27,500 \pm 1600$ years. The reason that two of the samples yielded only half of the computed amount can be explained as follows. Much of the sample consisted of bone material which had been in contact with fire; even though the burned bone pieces had been selectively isolated, some of the burned material must have been among the bones used for radiocarbon dating. Those pieces which were used for microanalysis were positively unburned and can accurately be used as a dating indicator. The three radiocarbon dates become progressively older from Layer 14 to Layer 21, indicating an undisturbed stratigraphy just as the N and U data.

Layer 21, which is representative of later Middle Stone Age dating to around 34,000 years, fits well into that time period. This suggests a transition from Middle to Late Stone Age around that time or a little later; this is also true for other sites in South Africa. Level 18, showing a discontinuity between the Middle Stone and Later Stone Age industries, dates this transition at Bushman Rock Shelter to around 32,000 years (UCLA-1755C).

By positioning the infant mandible in either Level 16 or 17 on the basis of microanalysis of nitrogen, it can be dated to 29,000 to 30,000 years (Table 2). This estimated age is based on the microanalysis of nitrogen.

The apparent age of the mandible suggests that the physical appearance and the state of fossilization are not clues to the age of a bone. Furthermore, a date of *c.* 29,500 years would make this infant mandible the earliest radiocarbon dated infant remains so far. It would also be the earliest dating of the transition of Middle Stone Age to Later Stone industries with a somewhat earlier date given by Beaumont & Vogel (1972) which places the transition at about 35,000 BC (Pta-422, $36,800 \pm 1000$ BC). The date of the

Table 2 Groningen-radiocarbon dates of Bushman Rock Shelter

Laboratory number	Depth (cm)	Stratum	Age (Years BP)
GrN-5874	15	Layer 3	9570 $\pm$ 55
GrN-4854	30	Layer 9	9510 $\pm$ 55
GrN-4813	61-69	Layer 12	9940 $\pm$ 80
GrN-4814	99-107	Layer 21	12,090 $\pm$ 95
GrN-4815	137	Layer 27	12,160 $\pm$ 95
GrN-5873	142	Layer 28B	12,470 $\pm$ 145
GrN-4816	142	Layer 28A	12,510 $\pm$ 105
GrN-5116	200	Layer 38	> 53,000
GrN-4855	225	Layer 41	> 47,500

UCLA-Radiocarbon dates of Bushman Rock Shelter

UCLA-1755B	127	Level 14	27,400 $\pm$ 1600
Infant Mandible	145 (?)	Level 16/17(?)	29,500
UCLA-1755C	160	Level 18	31,900 $\pm$ 1800
UCLA-1755D	178	Level 21	34,375 $\pm$ 4300



CM

Plate 2. Bushman Rock Shelter infant mandible compared with seven South African Negro infant mandibles of approximately the same age.



infant mandible is not an A_1 - A_2 date, since bones were dated that were not directly associated, but it is certainly better than an A_3 date. To be more specific, it could be called a A_2 - A_3 date since it can be compared relatively to samples above and below in the stratigraphy of the same site and then linked to absolute dates above and below.

When UCLA and Groningen dates are compared, the seeming discrepancy between dates can be explained in several ways. The two most obvious ones are contamination by recent material in older stratigraphic levels and secondly, disturbance of the rock shelter deposit in that particular part of the stratigraphy. Knowing the painstaking research at the Groningen laboratory, it is far more likely that stratigraphic anomalies exist between the different excavation locations dated by UCLA and Groningen. It would be interesting to collect and date unburned bone material directly associated with charcoal from the 1965 excavation, and burned bone samples which were dated by Groningen. The recent date on burned bone (GrN-4813) by Groningen seems to indicate that disturbance more than contamination is the probable cause for the recency of the Groningen dates.

2. Infant Mandible

The mandible is that of an infant between six to eight months of age. This estimate is based on the average time for completion of development of the crowns of the cuspid and first deciduous molar (Watson & Lowrey, 1969). Since variation in tooth development may be great it is not possible to determine the age more accurately. Moreover, assessment is based on standards derived from Caucasoid populations, since, to my knowledge, none is available for African infant populations.

The mandible consists of the almost complete right half of the corpus mandibulae and ramus, together with portion of the left of the corpus—fusion of the two halves is well advanced. The left ramus is absent and the corpus has been broken immediately posterior to the socket for the second deciduous molar. For the most part, therefore, the full depth of the corpus is preserved. The right ramus is complete, save that the condyle has been eroded on its antero-medial, posterior and lateral aspects and the tip of the coronoid process is missing. On the right side the alveolar bone has been partially broken on the lingual aspect of the socket for the first permanent molar and on the labial aspect of the sockets for the canine and incisor teeth. On the left side both lingual and buccal walls of the distal socket are defective as is the bone on the labial aspect of the sockets for the anterior teeth as well as on the buccal aspect of the first molar socket (Plate 1).

The crowns of the right deciduous lateral incisor, canine and molars are preserved intact—the crown of the second deciduous molar has not been completely formed.

The bone is light brown in colour and shows no apparent signs of mineralisation.

The mandible is broad in relation to its length [Table 3—estimated bigonial breadth (gogo) 51 mm and projective length of corpus (cpl) 38 mm]. The contour of the body as seen from above is angulated, the intercanine region being more or less flat and joining the rest of the body at a definite angle so that the contour is roughly U-shaped. The ramus forms a broad obliquely placed parallelogram [minimum breadth of ramus (rb) 19 mm] of moderate height [projective height of ramus (rl) 20 mm] with a moderately deep mandibular notch. The angle of the mandible is slightly inverted. The inferior border of the corpus is concave: it shows two projections, one formed posteriorly by the angle and one anteriorly by the symphysis menti. The symphysis is of moderate height [symphyseal height (h_1) 18.5 mm] and thickness (9.2 mm), the resultant index

Table 3

Comparison of Bushman Rock Shelter infant mandible with other Southern African infant mandibles. (Measurements are given in mm.)

Character	Bushman Rock Shelter (Present study)	Border cave (de Villiers, 1973)	South African Negro			(Present study)			Bambandyanalo (Galloway, 1959)				Oakhurst Shelter (Drennan, 1937)			
			A657 $\frac{5}{12}$ yr	A614 $\frac{5}{12}$ yr	A809 $\frac{5}{12}$ yr	A664 $\frac{7}{12}$ yr	A659 $\frac{8}{12}$ yr	A810 $\frac{8}{12}$ yr	A667 $\frac{10}{12}$ yr	K20 $\frac{4}{12}$ yr	K32 $\frac{4}{12}$ yr	K23 $\frac{6}{12}$ yr	K14a $\frac{10}{12}$ yr	M $\frac{6}{12}$ yr	N $\frac{6}{12}$ yr	O $\frac{6}{12}$ yr
h_1	18.5?	15.1?	16.9	16.3	17.8	18.1?	16.4?	16.1?	20.0	18.0	17.0	18.0	20.0	13.0	12.5	10.0
Symphyseal thickness	9.2	8.0	8.8	8.3	9.2	9.0	9.2	8.5	8.0	10.0	11.0	9.0	10.0			
Symphyseal Index	49.7	52.9	52.0	50.9	51.6	49.7	56.0	52.7	39.6	55.6	64.7	50.0	50.0			
Height at m_1	12.5	9.1?	11.6	11.9	12.9	12.8	14.1	12.6	14.4							
Thickness at m_1	9.0	8.4	8.0	8.1	9.1	8.1	8.5	8.0	8.9							
Robusticity Index	72.0	92.3?	68.9	68.0	70.5	63.2	60.2	63.4	61.8							
Height at m_2	12.1	11.1	10.7	11.1	11.8	10.1	13.1	13.1	12.6							
Thickness at m_2	9.4	8.8	8.7	8.7	9.1	9.4	10.2	9.1	9.5							
Robusticity Index	77.6	79.2	87.8	78.3	77.1	93.0	77.8	69.4	75.3							
zz^*	31.4	29.8	28.8	28.2	30.6	30.6	31.8	30.8	28.4							
ml^*	52.0?	51.0?	52.0		51.0?	—	54.0	55.0?	40.0?	58.0	57.0	60.0	63.0	43.0	40.5	42.0
cpl^*	38.0?	44.0?	41.0		40.0	41.0?	39.0	43.0?	40.0?							
rl^*	20.0	17.5	25.0		—	—	21.0	23.0	22.0?	22.0	21.0	22.0	25.0	15.0	13.0	14.5
rb^*	19.0	17.0	18.2		21.4	19.8	18.6	20.6	21.0	18.0	19.0	21.0	22.0	14.5	16.0	18.0
Rameal Index	95.0	97.1	70.2		—	—	88.5	82.4	95.4							
$M/\angle^*$	148°?	146°?	152°		148°	149°?	155°	143°?	150°?	139°	146°	133°	135°			
gogo	51.0?	45.6?	48.2		51.8	47.8	55.2	—	49.5	46.0	60.0	54.0	65.0			
crh	24.2?	19.0?	26.0		25.0	25.0	23.0	25.0?	27.0?					18.0	18.5	19.0

* Where available biometrical symbols are used.

being 49.7%. The symphysis is somewhat concave in lateral profile, the mental portion projecting slightly in front of the alveolar portion. The mental protuberance is prominent and roughly triangular in shape. The mandible shows on its anterior surface near the symphysis the depressions described by Hrdlička (1930) as mental fossae. These fossae are well developed due to a strong ridge along the inferior border which connects the mental protuberance with a small platysma tubercle situated below the canine alveolus. Two shallow digastric fossae are present. The single mental foramen is situated below the socket for the first deciduous molar and is directed superiorly and anteriorly. The upper part of the internal surface of the symphyseal region, the planum alveolare, is slightly inclined downwards and backwards and terminates in a faint ridge, the superior transverse torus. The genial tubercles are represented by a single small median ridge. The mandibular foramen has the typical infantile character of a circular aperture facing directly posteriorly. It is flanked medially by a blunt lingula, and leads off from a distinct gutter which is formed by the stress bar to the condylar process. The mylohyoid line is faintly demarcated and the mylohyoid groove is situated immediately below the margin of the mandibular foramen.

In Table 3 the measurements and indices of the Bushman Rock Shelter infant mandible are compared with those of other available infant mandibles of approximately the same age namely: Border Cave 3 (de Villiers, 1973); seven South African Negro; four from Bambandyanalo, Northern Transvaal (Galloway, 1959); and four from Oakhurst Shelter near George, Cape Province (Drennan, 1937).

Rightmire (1970) demonstrated by means of a discriminant analysis that the Bambandyanalo people fall within the range expected of the modern Southern African Negro and the Oakhurst shelter remains have been characterised as Khoisan (Drennan, 1937).

On a metrical basis it would be difficult to distinguish the Bushman Rock Shelter mandible from the South African Negro infant mandibles of approximately the same age, in particular A809, A664, A659 and A810. A657 and A614 are smaller and A667 larger in most of their dimensions. A657 and A614 probably represent somewhat younger individuals and A667 a slightly older individual. The Bambandyanalo mandibles are longer [maximum length of mandible (ml) 57 mm to 63 mm]; K32 and K14a are also appreciably broader [bigonial breadth (gogo) 60 mm and 65 mm respectively]. Whereas the Khoisan mandibles from Oakhurst Shelter are smaller in all their dimensions. The Border Cave 3 mandible is likewise smaller, but may well represent a younger individual.

The contour of the body as seen from above is angulated in all the South African Negro mandibles except A667, that is, the intercanine regions joins the rest of the body at a definite angle so that the contour is U-shaped as in the Bushman Rock Shelter mandible rather than divergent U-shaped as in A667, Bambandyanalo K20 and K23 (Galloway, 1959) and Border Cave 3 (de Villiers, 1973).

The rameal indices show all these African infant rami to be relatively broad but not as broad as in the San (Bushman) infant mandibles described by Wells (1931). The mandibular notch, too, is deeper in the Bushman Rock Shelter and South African Negro mandibles than in the San (Bushman) mandibles (Wells, 1931). As in the Bushman Rock Shelter specimen the angle of the mandible is slightly inverted in the South African Negroes A809, A664, A659, A810, A667 and slightly everted in A614 and Border Cave 3. In this respect the Bushman Rock Shelter and the six South African Negro mandibles, listed above, differ from the San (Bushman) mandibles described by Wells (1931) in

which the angle is distinctly everted. In the Bambandyanalo specimens (K20, K32 and K23) the angles are everted (Galloway, 1959).

The inferior border of the body of the mandible is concave in all seven South African Negro mandibles as it is in the Bushman Rock Shelter and Border Cave 3 specimens, showing two projections formed by the inferior end of the symphysis menti and the angle respectively (Plate 2). The inferior border, therefore does not show the sinuosity of the San (Bushman) infant mandibles as described by Wells (1931).

Although roughly triangular in the shape, the mental protuberance is less prominent in the South African Negro mandibles A664, A659, A810 and A667 than in the Bushman Rock Shelter mandible, consequently the profile of the symphysis menti is straight and more or less vertical rather than concave as in the Bushman Rock Shelter specimen. In the remaining three South African Negro mandibles (A657, A614 and A809) and in the Border Cave 3 infant, the mental protuberance is prominent and pointed. From Well's account (1931) it appears that in the San (Bushman) infant mandible the mental protuberance is less developed and less salient and that the symphysis menti is convex in profile.

The mental fossae and the ridge along the inferior border of the symphyseal region are well defined in five of the South African Negro mandibles: A657, A614, A809, A664, A810; in the Bambandyanalo mandibles K20, K23 and K32 (Galloway, 1959); in the Border Cave 3 mandible. The general development of these features in the five Negro, three Bambandyanalo and Border Cave 3 specimens is thus similar to that seen in the Bushman Rock Shelter infant mandible. The features of the planum alveolare and the superior transverse torus are likewise similar in the Bushman Rock Shelter and South African Negro mandibles (A657, A809, A664, A810, A659, A667). The genial region, on the other hand, is somewhat variable in these South African Negro infants. As in the Bushman Rock Shelter specimen, genial tubercles take the form of a small single median ridge in A614, A657, A659; A809, like the Border Cave 3 mandible, exhibits a single median genial pit and no genial tubercles; A810 has two superior and two inferior genial pits; A664 and Bambandyanalo K20, K23 and K32 two small superior tubercles and a single median inferior tubercle; and A667 has two superior genial tubercles.

As in the Bushman Rock Shelter and Border Cave 3 infants the mandibular foramen is circular in all the seven South African Negro specimens and is flanked medially by a short blunt lingula. The mylohyoid line is faint and the mylohyoid groove is situated immediately below the margin of the mandibular foramen.

Summary on the Bushman Rock Shelter mandible

(i) Metrically the Bushman Rock Shelter infant mandible cannot be clearly distinguished from the South African Negro mandibles of comparable age, but is larger than the Khoisan jaws.

(ii) The morphology of the Bushman Rock Shelter mandible likewise aligns it with the available South African Negro infant mandibles.

(iii) The Bushman Rock Shelter specimen is not only larger than the Khoisan mandibles of approximately the same age but shows none of the morphological features described as characteristic of the San (Bushman) infant mandibles described by Wells (1931).

(vi) The principal morphological differences between the Bushman Rock Shelter and Border Cave 3 infant mandibles lie in the contour of the mandible, as seen from above, in the form of the mental protuberance and in the morphology of the genial region.

Affinities of the Bushman Rock Shelter infant mandible

Although it has not proved possible, at present, to obtain an absolute date for the infant mandible, apparently found between the Later Stone Age levels 14 to 18 at Eloff's 1969 excavation of the Bushman Rock Shelter deposits, a date of 29,500 BP—determined on the basis of radiocarbon dating and microanalysis of nitrogen of bone samples taken from levels 14, 18 and 21—has been proposed by Protsch (1974).

The Bushman Rock Shelter infant mandible shows a cluster of metrical and morphological features which align it with the modern Southern African Negro infant mandible. With the San (Bushman) infant, the Bushman Rock Shelter mandible has no obvious morphological affinities.

The samples available for comparison were small and the specimens do not show considerable morphological differences. In these circumstances it is difficult to differentiate between small isolate group features and those characteristic of the regional population as a whole. However, features indicative of Negro affinity have previously been described in skeletal material found in association with Later Stone Age industries, namely at Inyanga, Rhodesia (Tobias, 1958); Thandwe and Kalembe Rock Shelters, Zambia (de Villiers, 1973). The Inyanga human remains are, to the best of our knowledge, undated. The radiocarbon date obtained for the Thandwe burials, AD 330 $\pm$ 115 (Phillipson, 1973), is broadly contemporary with the Negro Early Iron Age burials from Inyanga, Rhodesia (de Villiers, 1970) but the radiocarbon dates (Phillipson, 1973) for the Kalembe Rock Shelter burials are considerably earlier in time, that is, 8000 to 7000 BP for a fragmented adult cranium and mandible and 16,000 to 8000 BP for a fragmentary juvenile cranial vault.

A whole range of evidence appears to justify regarding the modern Negro and Khoisan populations as divergent specialisations of a single stock named Proto-Negro-Khoisan by Brothwell (1963), basic *Homo sapiens afer* Linn. by Wells (1969) and Protonegriform by Tobias (1972). Tobias suggested that the splitting of the proto-negriform Africans into the two major branches, the Khoisans and Negroes must have been relatively early in time "it is likely that the divergence had begun by the onset of the Late Stone Age . . ." If the dating can be confirmed, the Bushman Rock Shelter mandible may represent the infant stage of an early Negroid form of *Homo sapiens afer*,* exhibiting as it does apparent Negro characteristics. At the moment, however, the Bushman Rock Shelter mandible is an isolated find and final assessment must await further well documented and dated discoveries in Southern Africa.

We wish to thank Professor J. F. Eloff, Head of the Department of Archaeology, University of Pretoria for supplying us with the necessary bone samples for dating purposes and for the loan of the Bushman Rock Shelter infant mandible and generously allowing us to describe its affinities.

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* *Homo sapiens capensis* (Protsch, 1974).

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C. B. Stringer

*Sub-department of Anthropology,
British Museum (Natural History),
Cromwell Road,
London SW7 5BD, England*

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A Multivariate Study of the Petralona Skull*

The Petralona skull from Greece has been generally accepted as an Upper Pleistocene variant of Neanderthal Man. It was included in a series of multivariate analyses performed by the author on cranial measurements of Pleistocene hominids. The results of the Mahalanobis D^2 analyses suggest that Petralona is cranially similar to the Neanderthals, but facially is distinct. Overall it resembles the Broken Hill and Djebel Ighoud skulls most closely but there are features of resemblance to *Homo erectus* material. The results of these analyses support recent suggestions that the Petralona material is of greater antiquity than the Upper Pleistocene.

The Petralona skull was discovered in a stalagmitic deposit in the Clemontsi cave near Petralona, Greece, in either 1959 (Oakley, Campbell & Molleson, 1971) or 1960 (Bostanci, 1964; Poulanos, 1971). According to Poulanos (1971) the skeleton was also present at the time of discovery but was subsequently lost. The dating of the skull is extremely uncertain. It was apparently lying in an unstratified deposit and beneath it were implements said to be undiagnostic (Oakley, Campbell & Molleson, 1971) or early Mousterian (Poulanos, 1971). Bostanci (1964) considered that the skull and surrounding material had been re-deposited from elsewhere, possibly during Würm I, but Poulanos (1967, 1971, 1972) suggested that it was a burial of Riss-Würm or early Würm age. Earlier analyses of parts of the fauna excavated elsewhere in the cave had indicated an Upper Pleistocene date, but Schütt (1971) identified a hyaena resembling *Crouta crocuta praespelaea* amongst the material, suggesting a Cromerian (Günz-Mindel) date. Sickenberg (1971) using a more complete faunal assemblage concluded that the Petralona fauna could not be younger than the Mosbachian faunal complex (also found at Vértesszöllös) and could well be pre-Mindel.

Morphologically the Petralona skull has been accepted as a variant of the Neanderthal type (Kokkoros & Kanellis, 1960; Bostanci, 1964; Kanellis & Savas, 1964; Poulanos, 1967; Howells, 1967; Brace, Nelson & Korn, 1971; Brose & Wolpoff, 1971). Some workers noted atypical features resembling Rhodesian Man (Bostanci, 1964; Breiting, 1964; Yryson, 1964; Howells, 1967), Djebel Ighoud 1 (Suzuki, 1970) or even modern Man (Poulanos, 1972). Jelinek (1969) considered the skull to represent a very primitive example of Neanderthal Man, whilst von Koenigswald (1967) considered the occipital region of the Petralona skull was similar to Vértesszöllös—a suggestion which Thoma (1969) disputed. Kurtén (1972) and Hemmer (1972), aware of the revised dating of the Petralona fauna, emphasised the archaic characteristics of the skull. Hemmer suggested that it was an advanced *Homo erectus* form whilst Kurtén viewed it as a possible counterpart of the Heidelberg jaw and an early representative of *Homo sapiens*.

The present author was given permission to make a metrical study of the Petralona skull by the Geological and Palaeontological Institute, Thessaloniki, and it has been included in a series of multivariate analyses performed on fossil human crania. These analyses, primarily using the Mahalanobis generalised distance (D^2) statistic (Rao, 1952;

* Research conducted in Department of Anatomy, University of Bristol, England.

Talbot & Mulhall, 1962) were performed on combinations of measurements defined by Howells (1973), and additionally cranial angles (*ibid*) and other measurements were also employed. A total of 44 measurements and 6 angles were primarily used in a series of 14 analyses, but computational and other factors necessitated the use of a maximum of

Table 1 Variables used in analyses

Variable	Analyses in which used									
Biasterionic breadth	6	7	8					13	14	
Biauricular breadth		7	8					13	14	
M ¹ -alveolus radius				9						14
Biorbital breadth					10	11	12	13	14	
Ectoconchion radius				9	10					14
Bifrontal chord		7	8				12	13		
Frontomale radius				9				13		
Nasion-bregma chord	6	7	8							14
Nasion-subtense fraction	6	7	8							14
Nasion-bregma subtense	6	7	8							14
Glabella projection							12	13		
Glabello-occipital length		7	8					13	14	
Bijugal breadth							12	13		
Palate breadth						11		13	14	
Mastoid width								13		
Mastoid length								13		
Nasion radius				9	10					14
Nasio-frontal subtense							12	13		
Nasal breadth					10	11	12	13	14	
Nasal height						11		13	14	
Nasio occipital length								13		
Nasion-prosthion length						11		13	14	
Orbit breadth					10	11	12	13	14	
Orbit height					10	11	12	13	14	
Lambda-opisthion subtense	6		8							
Lambda-subtense fraction	6		8							
Lambda-opisthion subtense	6		8							
Bregma-lambda chord	6	7	8							14
Bregma-subtense fraction	6	7	8							
Bregma-lambda subtense	6	7	8							14
Prosthion radius				9						14
Supraorbital projection	6	7	8		10	11	12	13	14	
Subspinale radius				9						14
Bistephanic breadth	6		8							
Vertex radius		7	8	9				13	14	
Cheek height						11	12			14
Maximum cranial breadth	6	7	8					13	14	
Maximum frontal breadth								13		
Bimaxillary chord							12	13		
Zygomaxillare radius				9				13		
Zygoorbitale radius				9	10					14
Bizygomatic breadth								13		

25 variables at any one time. The measurements employed in the analyses reported here are listed in Table 1.

The contribution of variables to the generalised distances were also computed to enable patterns of variation to be examined. The analyses were performed on separate areas of the skull to allow the optimum use of less complete material and these areas were determined simply by which parts of the crania were most commonly preserved, rather than by functional criteria. Use was made of original specimens wherever possible but

casts were employed if the fossils were unavailable for study (e.g. Pekin, Steinheim and La Ferrassie). Measurements were also taken on a cast of the Steinheim skull reconstructed using the Swanscombe material as a guide. Although this was unsatisfactory in some respects it was included since it was more complete and less distorted than the original. Sample sizes varied according to the measurements employed, and for studies of the face

Table 2 **Samples used for Neanderthal and Upper Palaeolithic groups**

	Analyses in which included								
Neanderthal									
La Ferrassie 1	6	7	8	9	10	11	12	13	14
Gibraltar 1	6	7	8	9	10	11	12		14
La Chapelle	6	7	8	9	10	11	12	13	14
Monte Circeo 1		7		9	10	11	12		14
Le Moustier 1		7							
La Quina 5		7							
Spy 1, 2		7							
Upper Palaeolithic									
Arene Candide 1, 6	6	7	8	9	10	11	12	13	14
Arene Candide 4	6	7	8	9	10	11	12		14
Brno 3	6	7	8		10	11	12		14
Combe Capelle	6	7	8	9	10	11	12	13	14
Chancelade	6	7	8	9	10	11	12	13	14
Cro-Magnon 1	6	7	8	9	10	11	12	13	14
2		7		9	10	11	12		14
3		7							
Dolní Vestonice 3	6	7	8			11	12		
Engis 1	6								
Cheddar-Flint Jack's Cave 1	6								
Cheddar-Gough's Cave 1	6	7	8	9	10	11	12	13	14
Grimaldi 6	6	7	8	9	10	11	12	13	14
Kostienki 2	6	7	8	9	10	11	12	13	14
Laugerie Basse 2		7							
Lautsch (Mladeč) 1	6	7	8	9	10	11	12	13	14
5		7							
Maritza 2					10	11	12		
Oberkassel 1	6	7	8	9	10	11	12	13	14
2	6	7	8	9	10	11	12		14
Ortucchio 1	6	7	8	9	10	11	12	13	14
Predmost 3	6	7	8	9	10	11	12	13	14
4	6	7	8			11	12	13	
San Teodoro 3	6	7	8	9	10	11	12	13	14
Langwith 1	6	7	8						

or occipital area fell to 2 or 3 individuals in the case of the Neanderthals. Nevertheless it was considered preferable to use actual rather than reconstructed specimens wherever possible, and the generalised distances have been corrected for differences in sample size (Rao, 1952). The samples of crania for the Neanderthal and Upper Palaeolithic groups used in the analyses reported here are listed in Table 2. Numbering of the specimens is in accordance with the *Catalogue of Fossil Hominids* (Oakley, Campbell & Molleson, 1971).

The methodology employed in the study is reported fully elsewhere (Stringer, 1974) and will be described more extensively in a subsequent paper (Stringer, unpublished manuscript). The generalised distances were calculated in the normal way (a simple method was

described by Rightmire, 1969) and measurements of single crania were assumed to represent means for the population from which they were drawn. They were assigned a within-group variation on the basis of the average value derived from the pooled dispersion matrices of the larger samples. The assumption of homogeneity of dispersion matrices for this method can be questioned (e.g. Kowalski, 1972) but Van Vark (1970)

Table 3 Generalised distances (D^2) of fossil crania from the *Petralona* skull

Analysis No. of variables Area	6 13 vault	7 13 vault	8 17 vault	9 9 radii	10 8 face	11 9 face	12 11 face	13 25 skull	14 25 skull
Fossils									
Upper Palaeolithic	100.2 (21)	102.7 (23)	122.2 (19)	40.11 (16)	55.02 (18)	67.56 (20)	99.45 (20)	236.0 (13)	187.1 (17)
Skhul 5	41.66	40.50	50.14	16.70	N.S.	30.68	46.73	132.6	67.70
Omo 2	60.45	82.70	96.80	—	—	—	—	—	—
Djebel Ighoud 1	29.51	26.68	37.74	N.S.	N.S.	38.38	49.62	89.60	52.50
Rhodesian (Broken Hill)	N.S.	31.52	27.10	30.92	22.56	30.49	32.50	116.5	46.22
Amud/Tabun	—	33.03 (2)	—	17.15	28.66	25.40	57.09	122.4	71.90
Neanderthal	N.S. (3)	37.11 (8)	52.79 (3)	32.39 (4)	76.17 (4)	75.92 (4)	107.0 (4)	157.7 (2)	107.8 (4)
Krapina C	—	—	—	—	47.01	—	76.54	—	—
Saccopastore 1 and 2	N.S.	—	—	N.S.	27.05 (2)	28.53 (2)	—	—	84.40
Steinheim	—	79.60	—	—	67.29	101.6	89.20	—	120.4
Steinheim reconstr.	40.60	71.82	88.60	30.92	56.53	55.44	78.80	209.0	96.50
Solo	39.09 (4)	32.47	52.74	—	—	—	—	—	—
Pekin	27.02 (4)	49.09 (2)	60.15 (2)	—	—	—	—	—	—

Samples are of single specimens except where indicated by bracketed figures. Values are corrected for differences in sample size and are significant at the 5% level except where marked N.S. Analyses 13 and 14 on the complete skull used 37 different variables between them.

and Bilborough (1971) demonstrated practically that this assumption was reasonable for cranial data of later Pleistocene human populations, whilst Blackith & Reymont (1971) provided a more general reassurance on statistical grounds.

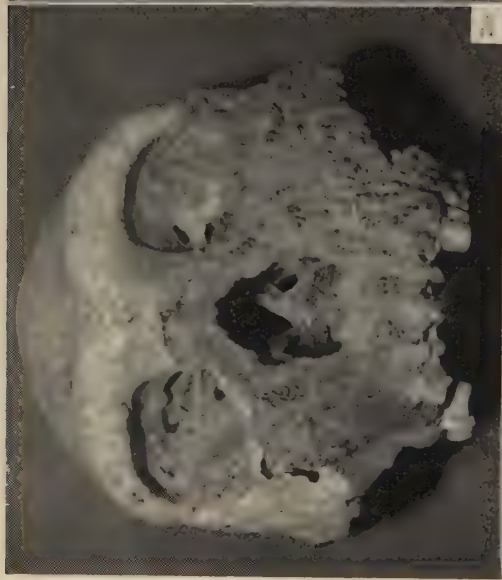
Some results taken from the generalised distances matrices are presented in Table 3.

As can be seen from the Table, the *Petralona* skull is closest to Djebel Ighoud, Broken Hill, Saccopastore 1 and the Neanderthals using vault data only. Analyses 1–5 of separate cranial bones showed *Petralona* to be of basic Neanderthal morphology but with a relatively high bifrontal chord, biauricular breadth and occipital subtense, and a low bistephanic breadth. In these features it tended to resemble the Pekin *Homo erectus* material. In analyses 6, 7 and 8, however, it was much closer to the classic

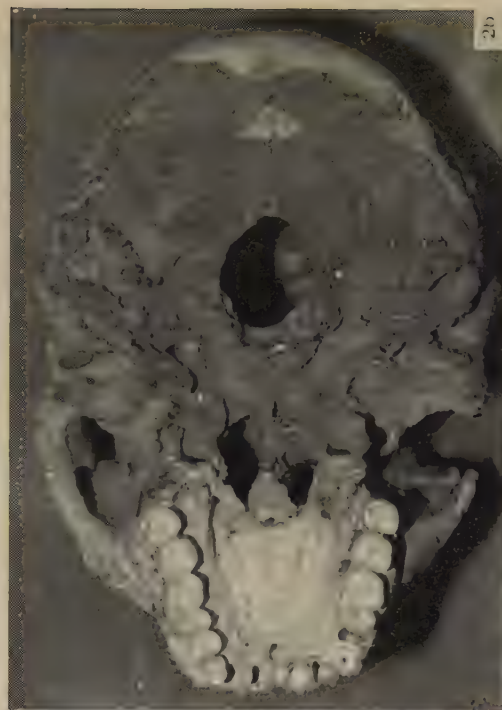
Plate 1. Petralona skull: right lateral view (approx. $\frac{2}{3}$ actual size).



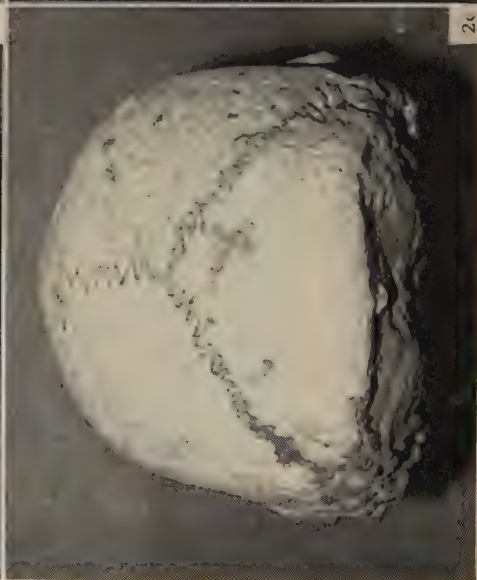
Plate 2. Petralona skull: (a) facial view (approx. $\frac{2}{3}$ actual size).
 (b) basal view (approx. $\frac{2}{3}$ actual size). (c) occipital view (approx.
 $\frac{2}{3}$ actual size). (d) vertical view (approx. $\frac{2}{3}$ actual size).



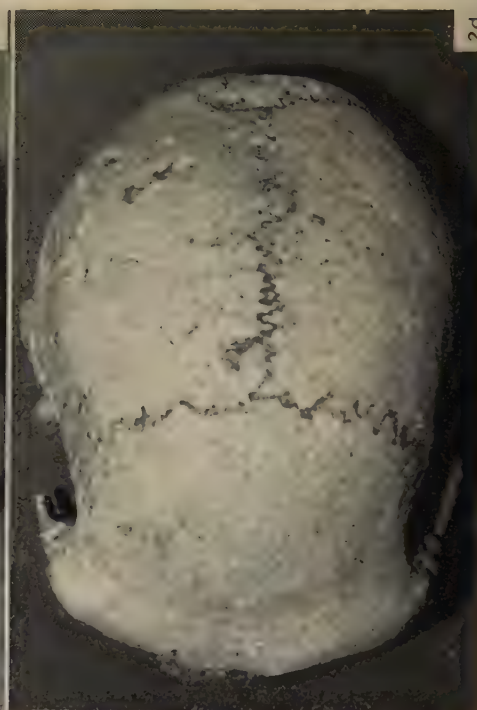
2a



2b



2c



2d

Neanderthals in terms of cranial height and breadth (although the actual position of the maximum breadth was much lower in Petralona), supraorbital projection, frontal and parietal form, and in occipital length than to the Pekin or recent *Homo sapiens* material.

Facially the Petralona skull is unique, since it is very distant from the Neanderthal and anatomically modern populations (represented by the Upper Palaeolithic group used here and also by large samples of recent crania measured by Howells). Although absolutely large in most dimensions, the Petralona face is particularly massive in the breadth of the upper face (bijugal, biorbital and frontomale breadths), interorbital breadth, the robustness of bone around the orbits, cheek height, and palate breadth (for example the biorbital breadth of the skull = 124 mm against a Neanderthal mean from six individuals of 108, $s = 4.28$). The dimensions of the Petralona mandible probably exceeded all known Neanderthal jaws in terms of bicondylar breadth (biauricular breadth of the skull = 156 mm against a Neanderthal mean from eight individuals of 133.75, $s = 9.65$), and arcade width (palate breadth = 88 mm against a Neanderthal mean from six individuals of 73.33, $s = 5.37$). Even the Heidelberg jaw is metrically too small to match the Petralona upper jaw and the closest matches amongst available Pleistocene material are with the "Pithecanthropus" IV palate, and the "Australopithecus" mandibles from Ternifine. The Petralona teeth are themselves not large although set in a robust jaw, strengthening comparisons with the Heidelberg jaw.

In addition to its massiveness, the orientation of the Petralona face differs from the classic Neanderthals. The inclusion of angles and radius measurements from the external auditory meatus in the analyses shows that Petralona is closer in these characteristics to Broken Hill, Djebel Ighoud, Saccopastore 1 and 2, Amud and Skhul 5 (the latter two crania with partly reconstructed faces). Computation of the nasio-frontal angle and zygomaxillary angle demonstrates that Petralona, like Steinheim, Djebel Ighoud and modern populations, has high values of these angles rather than the low values found in classic Neanderthal crania. This indicates that in Petralona medial parts of the face (nasion and subspinale) do not project forward from the lateral parts (frontomale and zygomaxillare) to the extent found in the classic Neanderthals. Further confirmation of this fact is provided by the relatively high zygomaxillare, ectoconchion and prosthion radius measurements, and the relatively low nasion, zygoorbitale and M^1 -alveolus radius measurements of Petralona. All these features link Petralona to the Steinheim and early Neanderthal forms which display relatively flat upper and middle faces but projecting lower faces, as also reported by Howells (n.d.). Additional differences from the classic Neanderthals include the deeply-set nasion, small orbit and nasal dimensions and a relatively large glabella projection—features which resemble earlier European fossils, Djebel Ighoud, Broken Hill and even Skhul 5.

When analysed using both cranial and facial measurements, the Petralona skull is very distant from the Neanderthal and modern *Homo sapiens* groups. Its closest neighbours in these analyses are Broken Hill and Djebel Ighoud. Its generalised distance from the Steinheim skull is large due to marked differences in cranial, facial, palatal and biauricular dimensions. Such differences in cranial morphology seem too great to be explained by sexual dimorphism alone, although more material would be useful here in the light of the variability shown by the Arago mandibles (de Lumley & de Lumley, 1971). Although the Petralona skull does resemble the non-classic Neanderthals such as Saccopastore and Amud, it seems likely that its much greater distance from the classic Neanderthal forms

and modern Man indicates that it is considerably older geologically, and is in fact a very early example of *Homo sapiens* or at least one that has retained archaic features in a way comparable to the Rhodesian skull. Compared to that skull, Petralona is more advanced cranially (with such features as a comparatively reduced occipital torus), but facially it seems more primitive. Photographs of the recently discovered Pithecanthropus VIII skull (Sartono, 1971) are reminiscent of Petralona in facial morphology, but cranially the Java and Pekin *Homo erectus* forms are more archaic. In a sense this tends to confirm previously held beliefs about the early European cranial material since Vértesszöllös, Swanscombe and Steinheim have all been claimed as advanced forms compared to contemporaneous material from elsewhere. However the Petralona skull, if it really is of pre-Mindel age, displays a facial morphology far more massive than that indicated by the (female) Pekin facial fragments and Weidenreich's reconstruction (Weidenreich, 1943). It is possible that whilst evolution of the cranial vault (in terms of cranial expansion, reduced robusticity etc.) proceeded at a faster rate in Europe than elsewhere, the reduction in size of the face may have been at a somewhat slower pace. Similarities between the new Arago mandibles (de Lumley & de Lumley, 1971) and the "Australthropus" material (Stringer, unpublished study) suggest that caution be exercised before proposing that European Middle Pleistocene human populations were evolving in isolation and at a faster rate than elsewhere. This assumption is still not warranted by the available material, and if Petralona and Pekin were known only from facial parts it is likely that the former might then be classified as *Homo erectus* and the latter as a primitive form of *Homo sapiens*.

Thus the Petralona skull cannot meaningfully be grouped with the classic Neanderthals, and it also seems very distinct from Steinheim, the most complete Middle Pleistocene skull from Europe. Overall it resembles the Rhodesian skull (which, like Petralona, displays "residual" *Homo erectus* features), and the recent re-dating of that fossil by Klein (1973) tends to support a close relationship between them. It also resembles Djebel Ighoud (a somewhat atypical Neanderthal fossil) and to a lesser extent the non-classic Neanderthals such as Saccopastore and Amud. Study of the new *Homo erectus* material from Java and the Arago skull may help to place the Petralona fossil amongst Pleistocene hominids, but provisionally it seems to represent a very early form of *Homo sapiens* comparable to the Rhodesian skull and is probably related to the Heidelberg and Vértesszöllös material from Europe. Chronologically it could well belong with a Cromerian (Günz-Mindel) fauna at Petralona but until more detailed archaeological and anatomical studies are completed, and the skull is adequately prepared (it is still partly encrusted with a calcareous deposit) this will remain in doubt. It is tempting to recall the words of Hrdlička about Rhodesian Man, when he admitted that he was "at a loss as to just where it belongs taxonomically or chronologically. It is a comet of man's pre-history" (Hrdlička, 1930).

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David S. Carlson

George J. Armelagos

*Department of Anthropology,
University of Massachusetts,
Amherst, Mass., U.S.A.*

Dennis P. van Gerven*

*Department of Anthropology,
University of Kentucky,
Lexington, Ky., U.S.A.*

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accepted 12 March 1974

Factors Influencing the Etiology of Cribra Orbitalia in Prehistoric Nubia

The present research represents an attempt to explain the occurrence of cribra orbitalia in Nubian skeletal remains associated with Meroitic, X-Group and Christian cultural horizons. The distribution of cribra orbitalia among 285 crania examined revealed a concentration of lesions among infants and aged individuals. While earlier studies have suggested cribra orbitalia may reflect the occurrence of abnormal hemoglobins such as sickle cell anemia or thalassemia, a consideration of the environmental context in which the lesions occurred makes an alternative hypothesis more likely. Particularly in Nubia (past and present), where parasitic infection is high, the diet is poor in iron, weanling diarrhea is frequent and multiparity is the norm, chronic iron deficiency anemia is a more likely causal factor. This interpretation is also compatible with clinical observations of cribra orbitalia among modern individuals suffering from chronic iron deficiency anemia.

1. Introduction

The analysis and interpretation of pathological conditions in human archaeological remains has suffered to a considerable extent from a lack of parity between the nature of the remains and the methods employed in their analysis. Many paleopathologists, trained primarily in medicine, have approached the analysis of skeletal remains from a clinical diagnostic model. From such a model, skeletal pathologies are viewed as unique cases. Cases are carefully described and an accurate diagnosis is attempted. Such an approach to skeletal materials which lack relevant soft tissue features as well as clinical histories has been of only limited value. As a consequence, many researchers in paleopathology have advocated the development of a wider-ranging populational approach. Specifically, it has been noted (May, 1960; Dubos, 1968) that there is a strong relationship between cultural, environmental and biological variables effecting the incidence of pathology in a population.

A more productive approach to paleopathological research, therefore, is one which incorporates biological, cultural and environmental variables in a single analysis. Adding to the need for such a broadened approach is the fact that most skeletal manifestations of pathology are highly generalized. With generalized skeletal manifestations it is necessary to rely on cultural and environmental variables if we are to understand the disorders themselves. This necessity is amply exemplified in the literature dealing with the generalized skeletal condition referred to as symmetrical osteoporosis.

Since the term "osteoporosis" has a general connotation for many bone conditions which show rarification, it has not been of particular value in describing specific types of bone lesions. In a recent review of paleopathology, Armelagos (1967) suggested three more definitive terms to be used in place of symmetrical osteoporosis. These are: (1) osteoporotic pitting, (2) spongy hyperostosis and (3) cribra orbitalia.

Osteoporotic pitting (Plate 1A) refers to lesions consisting of small pits on the external

* Present address: Department of Anthropology, University of Colorado, Boulder, Colorado 80302, U.S.A.

table of the cranium. This would correspond to the "porotic type" of Nathan & Haas (1966). Sometimes there is thickening of the diploic space associated with osteoporotic pitting, but it is rarely exaggerated.

Spongy hyperostosis (after Putschar, 1966), or hyperostosis spongiosa, (Plate 1B and 1C) is characterized by the appearance of osteophytes forming a network of trabecula-like bone on the external surface of the cranium. Thinning of the external table and expansion of the diploe is quite evident.

The term "cribra orbitalia" (Plate 2) referring to lesions on the superior surface of the eye orbits, was first utilized by Welcker (1888). Cribra orbitalia exhibits close ties in appearance to both osteoporotic pitting and spongy hyperostosis. Cribra orbitalia is produced by an expansion of the diploic space and corresponding thinning of the outer table, but is located exclusively in the eye orbits. In its less severe stages cribra orbitalia exhibits relatively minor porous openings in the orbital roof. In its most advanced stages there is considerable expansion of "honeycomb-like" cribrous bone into the area of the orbit normally occupied by soft tissue.

Numerous causes have been proposed for osteoporotic pitting, spongy hyperostosis, and cribra orbitalia both as generalized and specific conditions. Cribra orbitalia, in particular, has been thought of as a discrete trait (Brothwell, 1965) or as the result of pressure on the bones of the orbits due to hypertrophy of neighboring tissues and organs (Huhn, 1969). Perhaps the most prevailing interpretation, however, has favored the inclusion of all three conditions into one group labeled either symmetrical osteoporosis or porotic hyperostosis. Angel (1964, 1966, 1972) and Zaino (1967) have proposed hereditary hemolytic anemia as a primary cause of all three conditions. However, Angel also agrees with Moseley (1966) and Nathan & Haas (1966) that the same cranial lesions could be the result of a nutritional disorder.

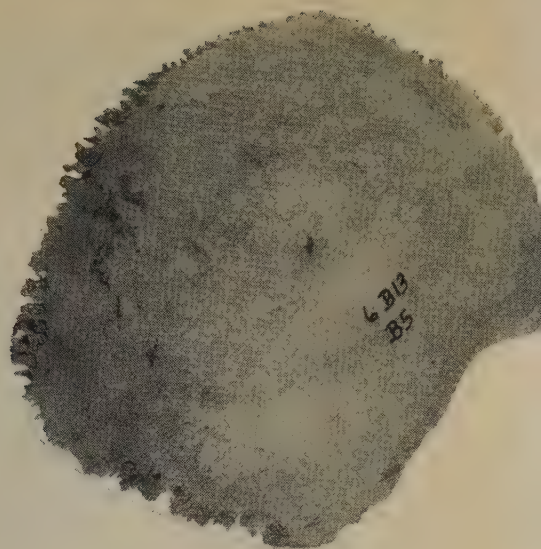
There are two hereditary hemolytic anemias, thalassemia and sickle cell anemia, which have been suggested as primary causes of cribra orbitalia as well as osteoporotic pitting and spongy hyperostosis. In these conditions, marrow hyperplasia of the diploic space in the cranial bones causes a thinning of the outer table and eventual outgrowth of trabecula-like bone. According to Moseley (1966) there is primary involvement of the frontal bone and orbits with subsequent spread to the parietals and occipital as well as to long bones and ribs.

As previously mentioned, nutritional disorders have also been suggested as a cause of cranial lesions resembling those produced in thalassemia and sickle cell anemia. Specifically, it has been noted by several clinicians and medical researchers (Moseley, 1966; Burko, Mellins & Watson, 1961; Britton, Canby & Kohler, 1960; Shahidi & Diamond, 1960) that iron deficiency anemia produces cranial lesions identical to those produced by hereditary hemolytic anemia.

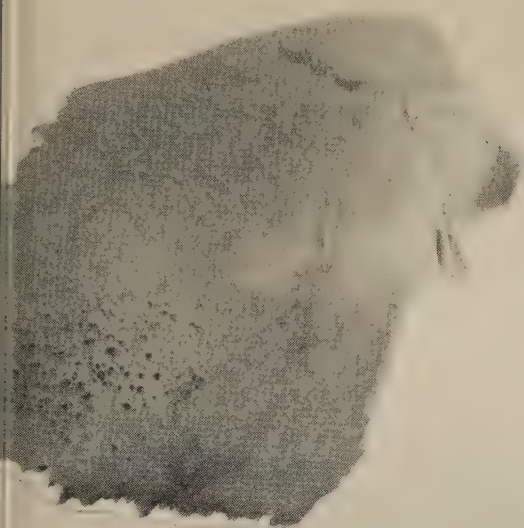
Hengen (1971), recently analyzed the occurrence of cribra orbitalia in 459 human skulls from areas of Europe as well as tropical and subtropical areas. The results of his investigation indicate a strong association between deficient iron intake, parasitism and the occurrence of this skeletal condition. Upon concluding his analysis, Hengen states:

"On the basis of these results and considerations it can be stated that iron deficiency anemias have the highest probability to be accepted as the general or chief factor in the etiology of the orbital spongy hyperostosis (cribra orbitalia). How far latent iron deficiency anemias became manifest in such cases by parasitic infestations . . . depends without doubt on the local conditions" (Hengen, 1971).

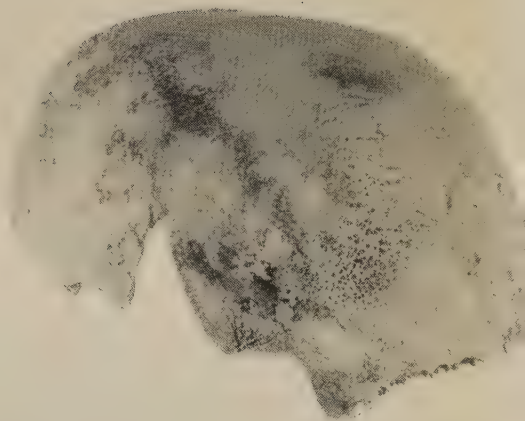
Plate 1. A. Osteoporotic pitting on the right parietal of an infant; B. spongy hyperostosis on the left parietal of an infant, C. spongy hyperostosis on the right parietal of an infant.



A



B



C

Plate 2. Advanced cribra orbitalia in an infant from the Nubian population.



It is apparent that any analysis attempting to explain the occurrence of cribra orbitalia, spongy hyperostosis and osteoporotic pitting in an archaeological population must take into consideration a wide range of environmental as well as biological variables. With this in mind, the present research represents an attempt to explain the occurrence of cribra orbitalia in Nubian skeletal remains associated with Meroitic, X-Group and Christian cultural horizons. Specifically, an attempt was made to evaluate the applicability of the iron deficiency hypothesis to the Nubian remains.

2. Materials and Methods

Data used in the present study was collected from skeletal remains associated with the Meroitic (350 BC–AD 350) X-Group (AD 350–550) and Christian (AD 550–1400) cultural horizons in Sudanese Nubia. Note was taken of all pathologies on the bony skeleton as well as information necessary for paleodemographic analysis. A total of 285 individuals were examined for cranial lesions. All data on pathology were initially analyzed by Armelagos (1968) and have been reported elsewhere (Armelagos, 1969).

While the Nubian remains have been separated into three cultural horizons, Adams (1964, 1965, 1968) has noted that there is marked cultural homogeneity with regard to subsistence technologies and economy over the period lasting from BC 350 to AD 1300, and, continuing up through modern times. The ancient Nubians, like their modern counterparts, were sedentary agriculturalists subsisting primarily on cereal grains, beans, dates and a few vegetables. Animals such as cattle, sheep and goats were used only to a limited degree (Adams, 1968).

3. Results and Discussion

The frequencies of osteoporotic pitting, spongy hyperostosis and cribra orbitalia were found to be disproportionate within the Nubian population. While the occurrence of osteoporotic pitting and spongy hyperostosis were quite low (4.3% and 0.7% respectively), the incidence of cribra orbitalia was high (21.4%). There was no post-cranial involvement associated with any of the three conditions and only one individual manifested more than one condition. In the one case both cribra orbitalia and spongy hyperostosis were present.

Since the frequency of cribra orbitalia was significantly higher than either osteoporotic pitting or spongy hyperostosis for the Nubian population, special note was taken of the age distribution of affected individuals (see Table 1). In the first age group, 0 to 10, 32% exhibited cribra orbitalia. The second age group, 11 to 20, showed a decrease in the frequency of orbital lesions to 11.1%. The frequency rose again in the last age group, 21 to 55+, to 19.9%. Thus, cribra orbitalia is present in relatively high frequencies throughout the entire age range of the population. However, it appears that infants and perhaps older individuals are more prone to exhibit cribra orbitalia than adolescents and young adults. Chi square analysis of the frequency distribution of cribra orbitalia within the three age groups gave a value of 16.35. On this basis, the probability that the observed distribution is random is $P < 0.01$.

Available archaeological and historic records, as well as modern ethnographic data can be used to provide the essential environmental context in which to interpret the occurrence of this pathological condition. Specifically, there is good evidence that

Table 1

Frequency of cribra orbitalia in prehistoric populations from Sudanese Nubia

Age	Number	Observations	%
0-10	24	75	32.0
11-20	6	54	11.1
21-55+	31	156	19.9
Total	61	285	21.4

$$\chi^2 = 16.35, P < 0.01.$$

conditions which give rise to a high incidence of nutritional disorders were likely present. Several researchers (Brothwell, 1967; Scrimshaw, 1964; May, 1961) have noted that poor diet, frequent parity and parasitic infection are all major factors which can result in such nutritional disorders as pellegra, kwashiorkor and iron deficiency anemia, the last of which has been shown to produce cranial lesions.

As previously mentioned, the diet of Nubian populations has remained remarkably consistent for roughly 3000 years. The diet was composed primarily of milled cereal grains such as millet and wheat, which contain critically little iron. May (1961) noted that 75 to 80% of the population of contemporary Egypt does not have an adequate nutritional intake and that iron deficiency anemia is common among infants and females. Prolonged sucking is common for Nubian children, as was likely the case in ancient Nubia as well. After weaning children ate cereal gruels, which contain almost no iron.

Evidence from paleodemographic analysis indicates a high incidence of mortality for females during the child bearing years, suggesting stress produced by a variety of factors including multiparity. The incidence of iron deficiency anemia among pregnant females in contemporary Egypt is high, occurring in 56% of all females according to May (1961). The probability that iron deficiency anemia will be present is high during pregnancy and increases with each additional pregnancy.

Multiparity and the level of iron deficiency anemia in a population are even more critically entwined since the iron level in both the mother and the fetus are affected. Infants are normally born with a reserve supply of iron which compensates for low iron content of mother's milk. Under normal conditions the supply lasts approximately six months, at which time an exogenous source of iron is necessary to ensure normal development. Although the physiology of iron transfer and the effects on the maternal-fetal relationship are not completely understood, it seems obvious that one or both must suffer due to a lack of iron.

A relatively high incidence of parasitic and bacterial infection is well documented for modern Nubia (May, 1961). Hookworm infection and schistosomiasis, in particular, are common in the area and it is unlikely that this differed in ancient Nubia. The effect of parasitic infection is devastating with regard to anemia due to internal blood loss and a general lowering of resistance to subsequent infections. Eng (1958), for example, demonstrated that hookworm infection causes the onset of iron deficiency anemia even when dietary intake of iron was more than is normally necessary.

All the above factors combine to cause a general syndrome found in infants known as "weanling diarrhea" (Stini, 1971; Behar, 1968; Scrimshaw, 1964). As the name implies, "weanling diarrhea" primarily affects infants who are just beginning to utilize sources of food other than mother's milk. In its most severe form "weanling diarrhea" causes extreme dehydration and malnutrition, often leading to the death of the infant.

Given the above evidence, it is extremely likely that iron deficiency anemia occurred in relatively large proportions of the population of ancient Nubia. The distribution of cribra orbitalia within the Nubian population also supports the iron deficiency hypothesis. It is during infancy and early childhood that individuals were most susceptible to parasitic infection and "weanling diarrhea", and would also likely have a poor nutritional intake of iron. It was also this age group which showed the highest incidence of cribra orbitalia. From adolescence through early adulthood we would expect an enriching of the diet and consequently increased resistance to the effects of infection. It was also during this time period that the frequency of cribra orbitalia decreased substantially. The higher frequency in the older age group can be attributed to several factors. The mortality of multiparous females is likely to be represented in this group, as well as older less resistant individuals.

Consideration of biological (physiological), environmental, and cultural variables leaves little doubt that cribra orbitalia in the Nubian remains resulted from iron deficiency anemia. Restriction of the lesions to the orbits, demonstrates that the condition, though chronic, was likely not to be severe.

4. Conclusions

It would be unfortunate if this analysis, like many earlier studies, fell into the trap of generalizing about the occurrence of cranial lesions such as cribra orbitalia in ancient Nubia to all populations where similar lesions occur. Rather than state categorically that cribra orbitalia is always the result of iron deficiency anemia, this analysis has sought to demonstrate that environmental and cultural, as well as biological factors must be considered if we are to understand the occurrence of pathological conditions in ancient populations. There is little doubt, especially in ancient Nubia, that thalassemia and sickle cell anemia could have been present and that they were likely to have been adaptively significant due to the possible presence of malaria. However, to assume that they are primary causes of the relatively high frequency of cribra orbitalia when a condition more common to the area produces the same effects on bone is questionable. In the case of cribra orbitalia in ancient Nubia, there is no reason to assume that iron deficiency anemia was not a primary factor in its etiology.

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Brunetto Chiarelli

*Istituto di Antropologia,
Universita di Torino, Torino, Italy*

Rory Daniel

*Department of Anthropology,
University of Toronto,
Toronto, Canada*

Cytogenetic Study of the Eskimo in Igloolik N.W.T. (Canada)

In January 1971 the chromosomes of 63 Eskimo individuals were harvested in Igloolik, Fox Basin, Canada. The study was attempted to elucidate any gross chromosomal abnormalities, the rate of chromosomal breakage and any chromosome polymorphisms peculiar to this isolated population.

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1. Introduction

The Eskimo population is of particular interest for biological study not only because of its successful adaptation to a stressful climate, but also because of the length of time the group has been separated from the ancestral Asian stock. While the Eskimo can first be identified as a separate group some 5000 years ago, it is believed the movement into the Arctic of peoples ancestral to the Eskimo and Aleut began 10–12,000 years ago (Hughes, 1973). A population such as the Eskimo can act as a model in the study of the biological variation which occurs in a population when it is under strong selective pressures for a considerable period of time. Moreover if we want to compare the Eskimo population with the European one, we can estimate a biological separation of at least 20,000 years which means a generation gap of 800–1000 generations, considering generation time as 20–25 years.

As part of the IBP-HA research project going on in the Eskimo community of Igloolik, N.W.T. (Canada), we had the opportunity to begin an extensive cytogenetic analysis in this settlement.

The purpose of our work was threefold. First we wished to detect any gross chromosomal abnormalities which might be present in the study subjects. Secondly, we wanted to observe whether there were chromosomal polymorphisms present in the population. Thirdly, we intended to look at and compare 'break' and 'gap' patterns in the Eskimo chromosomes with those of a control group.

We were stimulated to include this third aspect in our work by the hypothesis made by some workers that human populations not exposed to the various noxious chemical and mutagens of the industrial world would have a lower percentage of chromosomal aberrations than those exposed. Studies of the isolated Yanomama in South America, however, show that these people have an abnormally high rate of somatic chromosome breakage, probably due to environmental factors such as viral disease, or the people's use of the hallucinogen i.e. drugs, Ebene (Bloom & Neel, 1970).

To facilitate comparison of the chromosomes of the Eskimo and control (European) populations directly, and in relation to the above hypothesis, over half the cultures were

prepared using the blood of an Eskimo and that of an IBP team member of opposite sex. It was felt that preparation of the cultures in the field would help eliminate artifacts that can arise because of the delay which occurs in sending samples from the field; and that use of mixed cultures would help us identify any artifacts which would arise in our own work because of differences in the manipulation of the material during the preparation for the study.

2. Materials and Methods

As mentioned in a previous note (Daniel & Chiarelli, 1971) blood samples from 90 Eskimo individuals were cultured over a two week period in Igloolik in January 1971. The collection of our sample was random, though further analysis showed an occasional family grouping. The original sample included 46 females and 44 males ranging in age from 4–71 years. Two males have since been eliminated because of recording errors.

A total of 104 cultures were prepared, 53 % of them as mixed cultures. The blood of 4 individuals of European descent in the IBP team was used for the control cultures. An average of 5 slides were prepared from each culture. Two complete sets of slides were stained, one with ordinary Giemsa and the second with buffered Giemsa.

Nearly all the cultures harvested contained mitoses, however since we had no distilled water for the hypotonic solution (and had to use melted snow) a number of mitoses proved to be too clumped for adequate investigation. Cultures on two separate days gave such poor results that they had to be eliminated from our data. Thus, the actual sample for which we have material for study constitutes 69 individuals, about 15 % of the Eskimo population in Igloolik.

In the analysis are included only those individuals for whom we have karyotyped 5–20 well-spread mitoses taken from the two slides stained for each individual. Karyotyping was done according to the Denver Convention. Over 400 Eskimo karyotypes were prepared and another 100 for the controls.

The banding techniques of trypsin and quinacrine fluorescent staining have been applied to a small number of slides in a preliminary analysis.

3. Results

In none of the 69 individuals for whom karyotypes are available were there found any gross chromosomal abnormalities such as those related to pathological conditions which arise from sex or autosomal aneuploidy or structural aberrations. There were, however, some plates with an aneuploid complement. A brief analysis of these plates showed that in those cases in which the individual could be identified (in mixed cultures) there was no significant difference in the Eskimos and controls in the frequency of aneuploid cells (Table 1).

Table 1 **Aneuploid cells in both Eskimo and control individuals**

	Hypomodal	Hypermodal	Total cells	% Aneuploid cells
Eskimo	17	9	417	6.2
Control	4	2	102	5.9
Unidentified plates*	8	5	13	

* Unidentified plates refers to plates of individual in mixed cultures which could not be identified with certainty.

Fig. 1. Iskhung chromosomes treated with Quinacrine: (a) metaphase plate of a male; (b) the bright fluorescence of the long arm of the Y chromosome; (c) nuclei of leukocytes after Quinacrine treatment; the bright spots indicate the Y chromosome.

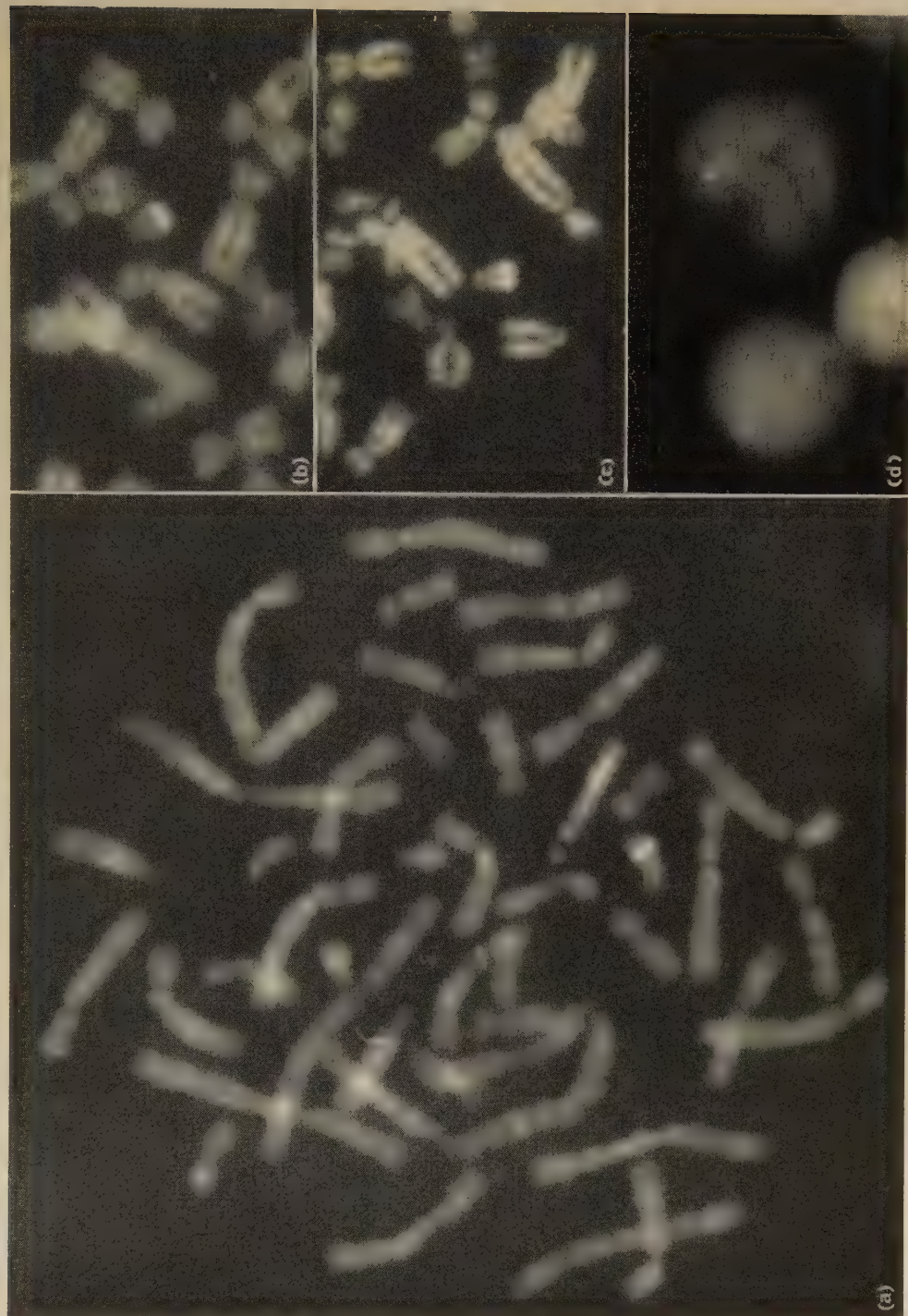


Plate 2. Variation in the length of the short arm and change in the centromeric index in the 22nd pair.

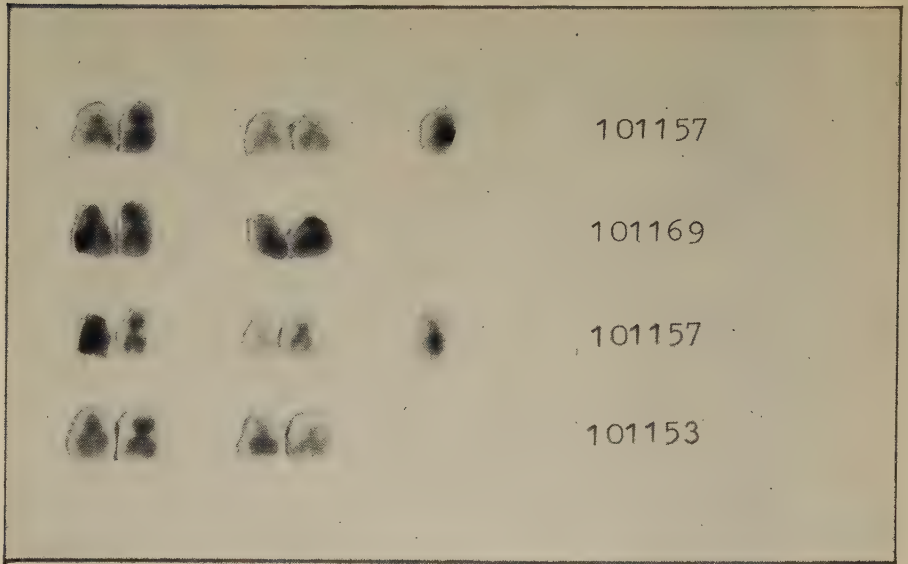
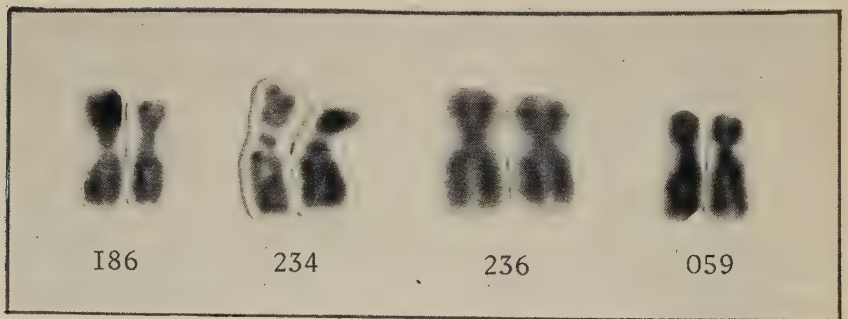


Plate 3. Different types of "gaps" occurring in chromosome 9.



The Eskimo karyotype did not differ significantly from the standard of the normal human karyotype (Denver, 1960) nor from that of the co-cultured control individuals.

Studies of chromosome banding in this population are only at a preliminary stage, but if small structural changes are present in the Eskimo chromosomes they could be detected by these techniques. The highly fluorescent region of the Y chromosome is detectable in males in this population (Plate 1).

The second aspect of our study involved detection of chromosomal polymorphisms in the population. Using the traditional techniques the following observations were made:

(a) Variation in the size of the Y chromosome is observable, however this chromosome is never as large as those in the F group. Because of this factor and of difficulties with the geneological data of the Eskimo, a family study was not carried out.

(b) A noticeable variant occurs in the length of the short arm in a G group chromosome. In a preliminary investigation it was thought this chromosome was a metacentric Y present in two males. Further analysis showed, however, that this chromosome was present in another male and three females. Family studies showed one of these females to be the mother of the two original males, thus this chromosome belongs to the G group. Family data are not available for the other individuals (Plate 2).

(c) Heteromorphism in the size of chromosome 16 occurs unusually consistently in the plates of 17 Eskimo individuals. This phenomenon does not appear to be related to the position of the chromosome on the plate. The biological significance of this variation is not clear.

(d) Variation in the secondary constriction of chromosome 9 is apparent. These constrictions vary their expression between individuals and between homologues. They were found in both the Eskimo and control individuals.

Further evidence of chromosomal structural variation in the Eskimo population may appear, as we mentioned, as a result of the banding study. The use of mixed cultures will facilitate comparison of the two groups.

The third aspect of our work involved elucidation of frequencies of small morphological differences in the chromosomes of the Eskimos and control individuals, differences related to heterogeneity in the staining along the chromosome filament.

This characteristic of chromosomes is traditionally treated under the heading of "chromosome breakage", however, we have not regarded it in this traditional way. In our analysis we have included all occurring achromatic 'gaps' in the stained areas and also very lightly stained areas along the chromosome arms. We have divided these features into two groups: those supposedly randomly distributed, and those which occur in specific localities on both the arms and in some cases also the homologues of only certain chromosomes.

The data were inadequate to give accurate frequencies of these random 'gaps' in the chromosomes, since 100 plates minimum per individual would have to be analysed. However, in order to obtain a general picture the data were pooled into the Eskimo and control groups and frequencies of random 'gaps' in each were compared. All chromosomes were considered, and 'gaps' occurring on sister chromatids were scored as '2'. As Table 2 indicates the frequency of gaps per plates does not differ significantly in the two groups.

Concerning the second group of non-random 'gaps' the following observations were made (see Table 3). In two Eskimo individuals a lightly stained area is found in the subterminal region of the 'p' arm in chromosome 1. This characteristic was observed in both sister chromatids and homologues. A few individuals exhibit an achromatic

Table 2

Random "gaps" observed in Eskimo and control chromosomes

	Total plates studied	St	C	M	Total	Freq. gap per plate
Eskimo	417	14	45	32	91	0.22
Control	102	3	7	9	19	0.19

Table 3

Number of plates containing non-random "gaps"

Chromosome	Eskimo		Controls	
	Homologues	Sister chromatids	Homologues	Sister chromatids
I(A)	I	3	—	I
I(B)	2	10	—	3
9	6	50	1	19
16	5	22	2	6
17	7	7	2	4

region associated with the centromeric region in the same chromosome. 'Gaps' occur both above and below the centromere in chromosome 16.

An interesting phenomenon occurs in the long arm of chromosome 17 in a number of plates. This phenomenon, which is an achromatic or lightly stained region in the median area of the long arm, occurs in the plates of 5 Eskimos and 3 controls. In mixed cultures where this characteristic occurs it usually appears in both individuals.

In chromosome 9 'gaps' appear in 4 different configurations. In some cases the entire secondary constriction is lightly stained or achromatic; in others where no secondary constriction is apparent, only a small area immediately above the centromere is unstained. In a number of cases the area below the secondary constriction is unstained, while in a few plates the centromere is stained and there is an achromatic region both above and below it. These phenomena appear in both sister chromatids and homologues (Plate 3).

4. Discussion and Conclusion

A number of cytogenetic analyses have been carried out on semi-isolated and isolated human populations. These include studies of the Greenland Eskimo (Barnicot & Travers, 1963; Carles-Trochain, 1971); the Ainu, Orok and Gilyak of Hokkaido and Sakhalin (Hungerford *et al.*, 1969); the people of Tristan da Cunha (Hamerton *et al.*, 1965); the Todas of South India (Chandra & Hungerford, 1966); New Guinean natives (Hungerford *et al.*, 1965); a group of Pygmies in the Congo (Cavalli-Sforza *et al.*, 1969); a small number of West Africans (Barnicot & Travers, 1963); the Hottentot (Heltne & Singer, 1971) and the Yanomama (Bloom & Neel, 1970). Chromosome abnormalities found in the Yanomama have already been briefly mentioned. In the Hottentot work it was reported that heteromorphic chromosome pairs and an 'extra chromatin fragment' occur consistently in some individuals. It is uncertain whether or not these results are an artifact of the culturing technique.

In all these studies except that of the Hottentot the culturing was done in a specialized laboratory away from the field after a delay of a few days. The advantage of our work is that it was performed in the field (in the world's most northerly cytogenetic lab!) and involved the use of controlled mixed cultures.

The data we have collected have not supplied us with any very unusual results. That there were no individuals found with gross chromosomal abnormalities is not surprising, mainly because of the limited sample and the fact that all the individuals studied appeared clinically normal. It also seems reasonable that there would be strong selective pressures working against abnormal individuals in this population, as though the Eskimo become more sedentary this pressure loses much of its importance.

All the chromosome variations observed in the Eskimo chromosomes are comparable to those found in other human populations. An analysis of the different frequencies of these variations in populations has not been carried out except for the 'large' Y chromosome (Soudeek, 1973).

The problem of chromosome breakage could be of some ecological interest as chromosome analysis can supply some information on genetic damage that has occurred in a population due to its exposure to deleterious substances in the internal and external environments. However, it appears that the traditional approach to the problem of breakage may have to be revised on the basis of new concepts arising from increased knowledge of chromosome ultra-structure and relationships involving the chromatid filament and nuclear membrane (Chiarelli, 1973). Rather than being actual 'breaks' or 'gaps' in the chromosome filament these achromatic and lightly stained areas may be due to inactivation of protein synthesis in a particular area, or to differences of coiling. Revision of the breakage concept is also indicated by the work of Caspersson *et al.* (1972) which shows that chromosome 'breakage' seems to occur more frequently in lightly stained areas of banded chromosomes treated by fluorescent staining procedures.

The most important aspect of our work, we feel, rests on its most obvious finding: that of the homology of the Eskimo karyotype with that of directly comparable European controls. These data support other data on the seemed stability of the human karyotype, a stability maintained in spite of the differentiation of mankind into various, more or less, distinct populations.

The more refined techniques of chromosome banding applied to individuals of various populations, especially isolated ones, and in the context of the mixed culture could add to the reliability of this statement on homogeneity. In any case results of this kind of study would have major evolutionary and ethical implications.

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James Hamilton

Department of Zoology,
Duke University,
Durham, N.C. 27706, U.S.A.

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Hominid Divergence and Speech Evolution

Hominids evolved from a population which diverged from other hominoids during the Mio-Pliocene. This population was perhaps forced by ecological conditions and competitive exclusion to rely more on tools, gathering, hunting, vocal communication and memory, under whose mutually positively reinforcing effects the hominids diverged. The ape ancestors may have been forced into the forests (or they may have forced hominids onto the savanna), while hominids adapted to a plains, hunting econiche.

Speech was selected for because verbal symbols served as retrieval cues for a large number of complex concepts and were transmissible, and thus could be used to influence food-getting and other behavior by the social group.

Speech is dependent on three inherited entities: (1) anatomical and neurological adaptations which allow vocalization of a wide range of phonemes in rapid succession and which allow for (2) duality of patterning, thereby promoting a large number of words, and (3) encoding, which greatly increases the rate at which verbal information transfer can occur. Speech may have evolved through small hominid groups using progressively more phonemes in an increasingly blended manner, with encoding subsequently being selected for. Neandertals apparently could not encode speech and could speak only a restricted range of phonemes. Their expanded cranial capacity may have been selected for to store ambiguous and slowly transmitted verbal data.

The hominoids—chimpanzees, gorillas and humans—have apparently all evolved from a common ancestor, *Dryopithecus*, during the past some 5–15 million years. The field of human evolution is especially concerned with the particular ecological features which have selected for the behavioral and structural traits found in the divergent hominoid line which evolved into *Homo*. Alternatively, the problem of hominid divergence from dryopithecines could be turned around in asking instead: Why have not the other hominoids evolved the human capacities for complex communication and culture?

Hypothetically, competition in a common environment among sympatric populations of the ancestor species of the *Pongidae* and *Hominidae*, along with competition from other Primates and carnivores, may have induced a divergence which led to varied econiches for hominids and apes. The geographical econiche distribution of contemporary Primates seems to indicate that competitive exclusion has been extensively operating. Gorillas, for example, live in mountainous regions sequestered from most humans, and are largely vegetarian and completely non-carnivorous. While chimpanzees are quite suited to a terrestrial environment, they have retreated into forest environments in every region where they have been sympatric with modern humans. Chimps can bipedally walk and run easily and efficiently (Taylor & Rountree, 1973) and in areas uninhabited by humans actually live in the open savannah and may travel long distances between tree groves (Kortlandt, 1962). Baboons are also terrestrial plains-living animals and, like humans, are carnivorous hunters. Humans and baboons may have seriously competed for similar food sources (including seeds, roots and plants, as well as animal prey) at times in their phylogenetic histories. It has been postulated, for example, that ecological competition through human hunting may have caused the extinction of a certain lowland baboon

Simopithecus subgenus which existed from 5,000,000 to 50,000 years BP (Anonymous, 1973).

A slightly unequal reliance on different food sources (Jolly, 1970) and an incipient tool use may have enabled hominid ancestors a competitive advantage in plains survival while other terrestrial apes come to rely more on woodland-forest environments. Conversely, the pongid ancestors might have competed more successfully in the forest-woodlands and edged the protohominids onto the plains. Probably each group tended to exclude the other from its predominant econiche. Regardless of who pushed whom out, once these populations began exploiting different econiches, the resulting allopatry would promote further divergence by limiting gene flow. Just as there are today two species each of both chimps and gorillas, so in the Miocene-Pliocene, diverging allopatric populations of hominoids coexisted (Frayer, 1973).

It is somewhat debatable whether dietary specializations or incipient tool use came first—and which was the primary reason for the initial hominid divergence (cf. Jolly, 1972). There is little doubt, however, that once econiche diversity for Miocene apes was effected, the different econiches provided varying opportunities and selective pressures for culture, i.e. tool use and vocal communication, and that culture was instrumental at some point in influencing the divergence of proto-hominids and other hominoids. A forest-woodland environment probably did not select for a complex tool-speech-hunting-gathering culture among pongid ancestors. Schaller (1963), for example, observed gorillas in a natural habitat of thick evergreen vegetation where food was omnipresent and easy to get and where rocks, sticks and other potential tool materials were rare. Young gorillas in captivity resemble chimps in their curiosity in manipulating objects, and can learn to accurately throw food and dirt at people. Gorillas, like chimps, assume a two-legged posture during weapon use and use sticks and clubs. Yet gorillas display such behavior in the wild rarely, if at all, probably because they do not have to use tools to protect themselves against predators or to find food. On the other hand, savannah chimps live in an econiche where food is seasonal, scattered and hard to get, and where tool material is readily available. Itani & Suzuki (1967) have opined that only savannah-woodland, but not forest chimps, make tools. Thus tool-use is perhaps a function of habitat (Kortlandt & Kooij, 1963; Lancaster, 1968). Just as contemporary chimps stalk infant baboons, monkeys and antelope, australopithecines also may have preyed on these species (Broom, 1950). While the evidence for extensive australopithecine hunting is ambiguous (Wolpoff, 1973), and while some australopithecines at times may have even been the prey of large carnivores (Brain, 1970), there is good evidence that australopithecines used bone clubs to hunt baboons (Dart, 1949). Geological evidence indicates that the climate at Olduvai Gorge was relatively dry throughout much of the time that the beds bearing australopithecine fossils were deposited, and that desert or semi-desert conditions may have prevailed at least twice (Hay, 1963). Food may have been at times scarce on the parched savannahs, and australopithecines may have been forced to turn to predation. In order to effectively hunt certain species, australopithecines may have found it highly advantageous to use clubs and bipedal locomotion. While chimps hunt infant baboons well enough without clubs, australopithecines apparently preyed on larger baboons, which made club use highly advisable. Chimps can use clubs with a two-legged upright stance and attack leopards with sticks but they do so only as a means to drive away predators. Perhaps a scarcity of food also induced a greater use of digging sticks for uncovering insects, as among contemporary chimps, or for digging tubers or roots. Thus, a greater use of tools by

australopithecines in a savannah environment over that of chimps would indicate that while the same type of behavior may have been present in the phylogenetic histories of both groups, it was carried further by human ancestors than by chimp ancestors.

Apparently non-verbal communication is sufficient to coordinate hunting behavior and direct others to food among modern woodland-forest chimps (von Lawick-Goodall, 1971; Menzel, 1971). Not only might vocalization have been of little use, it might actually be dangerous in a forest environment where predators can hide among thick vegetation, detect distant vocalizations and use them to track down young chimps. Chimp mothers are quite careful about their offspring's safety in the potentially dangerous forests and keep them near by for several years after birth. Also, the need for chimps to aurally detect the approach of predators might necessitate a low level of noise (Kortlandt, 1962). On the other hand, these constraints against vocalizations would not hold in a savanna environment. Vocalization, like tool use, may be ecologically favored in savanna, as opposed to forest-woodland environments.

Although the ape population which later gave rise to hominids was at first interfertile with other ape populations and morphologically undifferentiated, a cumulative process of cultural innovation, reinforced by econiche isolation and genetic adaptation, may have increasingly diverged the protohominids. Initially, local innovations and minor cultural variations in tool use and food getting behavior may have developed among the various hominoid populations in a manner somewhat analogous to gene drift among small isolates. For example, cultural differences in tool use may be seen among allopatric populations of chimps. Ivory Coast chimps, who use nut-cracking sites and sticks for cracking nuts (Struhsaker & Hunkeler, 1971), do not fish for termites with prepared twigs, as do Tanganyikan chimps (van Lawick-Goodall, 1971). Conversely, Tanganyikan chimps have not been reported to use nut-cracking tools and sites. A multiplicity of such cultural differences have been documented for a variety of Primate species (Crook, 1970), and are due to a process labeled "tradition drift" by Burton & Bick (1972)—a fortuitous learned behavior by an individual animal may lead to its adoption by the entire troop, depending on its adaptive value and on the influence and dominance status of the innovator. Once the mechanism of cultural transmission was initiated, the mutually positively reinforcing effects of culture and morphology on one another may have led to increasing divergence among the hominids. This process, termed deviation amplification, helps one conceptualize how hominid behavior may have influenced this taxon's evolution with an increasingly greater effect over time (Maruyama, 1963; Bajema, 1972; Bielicki, 1969; Holloway, 1967). A cultural and genetic divergence with geographical isolation similar to the model of hominid divergence suggested here, may have occurred in the case of the European neandertals, for example. Similarly, a cultural and genetic divergence along with geographical separation perhaps differentiated the robust and gracile varieties of *Australopithecus* and *Homo habilis*. Cultural differences in presence or absence of tools, tool type, size and in tool material among the various hominid sites in East and South Africa, concomitant with striking morphological differences, have been well documented (Isaac *et al.*, 1971; R. Leakey, 1973a, b; Merrick *et al.*, 1973; Tobias, 1971, pp. 134-36). The finding of depressed fractures in skulls of Miocene animals suggests tool use in hunting (L. S. B. Leakey, 1968), and implies that cultural divergence was already proceeding at this time among hominoids.

Influencing the behavior of others, particularly in food-getting situations, may have provided the primary selective pressure which led to the association of constant meaning

with sounds and to a control over sound emittance in the hominid line (Buettner-Janusch, 1966, pp. 335–39). Directing the attention of others involves the social interaction of a number of individuals simultaneously, and is thus an ideal situation in which a standardization or an understanding of a certain vocalization might occur. Mobile male chimps often vocalize loudly and drum on tree trunks in proportion to the amount of food they have found, which attracts less mobile females with infants to the feeding site. Furthermore, exploring males often influence other chimps to travel to other feeding spots (Reynolds, 1967, pp. 128–132). Chimps have the capacity to convey to other chimps the presence, direction, quality and relative quantity or preference value of distant hidden objects which they have not seen for several minutes. The mode of information transfer does not involve complex ethological displays or language and does not result from human training (Menzel, 1971). It probably depends on both gestures and soft vocalizations. At any rate, it is easy to visualize an australopithecine male group running down an antelope, baboon or similar prey and then calling for the young and females to join them. If a scouting hominid found edible seeds, leaves or other food, it would be very selectively advantageous for it to be able to indicate to troop members where the food is and influence them to follow.

Speech ability probably evolved under ecological conditions selecting for a wide range of communal, involved behavior—food gathering, hunting, social organization, tool-making—and thus the best evolutionary strategy was elaboration of a mechanism which motivated relatively long-term efforts by the social group, involving memory of goals and information over time. Speech facilitates memory of individuals in reinforcement and response delays; Spiker (1956), for example, found that youngsters who had learned distinct names for certain stimuli performed better in delayed response tests than youngsters who had been given only discriminative training with these stimuli. Barnett *et al.* (1959) obtained comparable results with mentally retarded children. These two studies suggest that verbal names permit a mental representation of an absent stimulus during a delay.

Another important selective value of speech is its enormous utility in concept formation. Verbal symbols can serve as retrieval cues for complex concepts and provide for great economy of effort in thinking about and communicating absent stimuli and concepts. Evidence for this comes from, for example, experiments showing that hearing youngsters perform better than preverbal deaf youngsters on concept formation and similar mental tests (cf. Church, 1961, pp. 152–53). Presumably, plant gathering and hunting hominids had to simultaneously consider many complex, ambiguous concepts, e.g. maintaining constancy of social and sexual relationships, classifying animals according to their food habits, habitats, desirability, difficulty of hunting, tracks and spoor, and location of hunting grounds, water sources, edible plants, camp sites and materials for tools. One example of a concept being mapped by and existing before language learning is that of similarity and dissimilarity by Premack's chimp, Washoe. Washoe apparently had concepts of "is the same as" and "is not the same as" since after training with specific instances of each concept, she could generalize this concept to relations between other pairs of objects as well (Premack, 1970; Premack & Premack, 1972).

There is evidence that nonhuman Primates can form concepts as well as or perhaps better than humans, when the humans do not use speech. Monkeys and apes, for example, can without great difficulty solve discrimination problems with three conditions of ambiguity, which many humans of sound mind cannot solve ("ambiguity" refers to potential confusion as to what cue factor(s) is rewarded; e.g. position, color or size cues of the objects

to be discriminated). Even more complex problems can be mastered by nonhuman Primates; one chimp has solved tasks with five reward ambiguities, and rhesus monkeys can attain human-like performance in color concept formation (Harlow, 1951, 1958, p. 281). Probably human subjects would have little opportunity to associate verbal stimulus clues with stimuli in discrimination tests with one or more ambiguities. It is cogent here that chimps have been assessed, on the basis of psychological testing and empirical observation, to possess the mental capacity of about a three year old human, who is generally without extensive speech abilities. The fact that chimps can use English syntax in manipulating plastic symbols to express pre-existing concepts, and can form certain ambiguous concepts as well as humans indicates that chimp conceptual capacities resemble those of humans; that humans are only more efficient at concept formation because they use speech. Many Primates besides humans have been found to possess culture, i.e. learned behavior which may be transmitted among individuals, so that culture should not be considered to have arisen only among hominids. But speech may be considered to be a human specific trait which enormously multiplied humans' capacity for culture by coding for concepts and allowing them to be accumulated and transmitted intergenerationally through learning.

As meanings became standardized through association with specific single sounds, the hominid vocabulary was probably rapidly used up. The number of vocalizations Primates can use is limited by both the vocal apparatus, which is capable of producing only a few sounds, and by the auditory neural wiring, which resolves sounds over a certain frequency range, and which cannot resolve sounds if their frequencies are too similar. Probably there was selection in both the auditory and vocal systems to enable hominids to produce and discern a number of distinct sounds, each possessing a distinct meaning. A communications system where the smallest units of sound are endowed with fixed meanings is termed a closed system, and its vocabulary is strictly limited to its number of individual sounds. An evolutionary strategy among both chimps, humans and other species to increase the number of words is duality of patterning, or the combination of phonemes which are themselves meaningless, to form words. As the number of meaningful sounds increased through evolution, probably some of these sounds were simultaneously blended and recombined to gradually produce an open communication system, with meanings, at first iconic, then progressively more arbitrary, being attached, through common understanding among small groups of hominids, to groups of two or maybe three phonemes. A model for this process is found among chimps, who have about 32 vocalizations which they use in a fluid manner, recombining them and using them variably to express different meanings and emotions according to social and environmental context (Yerkes & Learned, 1925). Both Washoe and Sarah have spontaneously created unique sequences of symbols with either sign language or plastic figures and thus expressed new meanings (Premack & Premack, 1972; Gardner & Gardner, 1969), a process somewhat similar to phoneme blending.

The evolution of an open phoneme system may have taken hundreds of thousands and most likely millions of years to reach its present level of complexity. The anatomical and neurological adaptations involved in the evolution of speech from early hominoids to *Homo sapiens* is immense. Sound spectrograms of gorillas, chimps and rhesus monkeys indicate that their vocalizable frequency range is too small for them to possibly produce human speech. And even if they could produce all human phonemes, they lack the ability to rapidly and easily produce successions of phonemes, as occur in human speech. Nonhuman Primates do not appear to change the shape of their supralaryngeal tracts by

varying their tongues during sound production. Their tongues are long and thin and thus are not structurally suited to the continuous variation of the vocal tract's cross-sectional area during speech by rapid lingual movements. Furthermore, the pharyngeal region, which is instrumental in human speech through its shape variation during speech production, does not exist in other Primates, since their larynges are positioned almost in line with the roof of the palate (Lieberman, 1968; Lieberman *et al.*, 1969, 1972; Lieberman & Crelin, 1971). The human vocal tract is less agile at swallowing and respiration than that of other Primates, and apparently the only function for which it is better adapted is speech; therefore, it must be hypothesised that there was, indeed, selection especially for vocalizing ability in human ancestors. This hypothesis of consistent evolution of phoneme producing ability would predict that hominid fossils show an increasing anatomical compatibility with a widening range of phoneme production. In fact, several comparative anatomical studies of fossil and living Primates suggest that anatomy parallels sound-producing ability and that the closer to modern adult *Homo sapiens* a specimen is, the more its relevant facial and cervical anatomy resembles that of modern humans. Generally, the earlier a hominid fossil is, the smaller its pharyngeal region (Negus, 1949; DuBrul, 1958; Lieberman, 1968; Lieberman & Crelin, 1971; Lieberman *et al.*, 1972).

Direct evidence for speech evolution is meager. Plaster casts of a gracile australopithecine skull compared with a chimp skull indicates that both species' vocal tracts are very similar and that there is room for only a very thin tongue. The vocal tract length is about the same for both specimens (Lieberman, 1968). Presumably, gracile australopithecines could not speak well if they spoke at all. Holloway's (1972) analysis of an especially well-preserved *Australopithecus robustus* endocast provides evidence for speech capacities among this taxon. Through close visual examination and metrical comparisons, Holloway determined that the 530 cc specimen evinced a larger and more rounded Broca's area and that the inferior parietal lobule is more expanded than in pongids, as are the posterior and interior portions of the temporal lobe, all of which are functional in speech. It seems reasonable to take this evidence of neural reorganization as indicating some speech capacity among robust australopithecines.

While duality of patterning enormously increased the hominid vocabulary, encoding greatly increased the speed at which verbal information transfer could occur. Humans are able to send and receive verbal data at a high rate due to an encoding and decoding process by which speech sounds are emitted and perceived in syllable-sized units, rather than by individual phonemes. The vowels /a/, /i/, /u/ and the glides /y/ and /w/ serve as the principal decoding signals in human speech. Information transmission systems which do not use human language phonemes, e.g. reading machines for the blind, or "hearing" machines for the deaf, work no faster than one-tenth the speed of human speech. This theory of speech encoding is not universally accepted by cognitive psychologists and linguists; yet it is supported by much evidence and is a quite useful tool in understanding human phonemic evolution (cf. Lieberman *et al.*, 1972). The ability to encode syllables depends on neurological characteristics and is thus, like supralaryngeal anatomy, genetically determined.

Lieberman *et al.* (1972) and Lieberman & Crelin (1971) have determined that neanderthals could not encode speech. La Chapelle-aux-Saints neanderthals, who lived about 100,000–35,000 years BP, on the basis of vocal tract area functions, cineradiographic data, the geometry and anatomy of cervical muscles and skull, and a computer implemented analogue of the supra-laryngeal vocal tract, apparently could not produce a range of

vowel sounds including /a/, /i/, /u/ and /ɔ/, or consonants like /g/ or /k/. Due to an inflexibility of the vocal tract, neandertals had fewer phonemes available to them, even though they had a greater phonemic range than modern non-human Primates. If neandertals were able to control rapid articulatory vocal tract shape and size changes to produce their attributed phonemes, then they may have possessed language. Since they could not pronounce /a/, /i/ or /u/, however, the principal encoding sounds in human speech, they probably could not encode speech, and thus vocal communication probably proceeded much more slowly than among modern humans.

Neandertals apparently possessed larger average cranial capacities than even *Homo sapiens*—about 1600 cc compared to 1450–1500 cc for modern humans (von Bonin, 1963). This larger brain size is puzzling since there is little obvious reason why neandertals should have had need of such an expanded brain. The apparently limited number of phonemes and phonemic contrasts available to neandertals may provide an answer. A small number of relatively identical-sounding phonemes transmitted slowly without encoding would probably be conducive to confusion of transmitted verbal information with a corresponding difficulty of memory storage. Capacity of memory storage has been correlated with brain size among various animal species (Rensch, 1957, 1972, pp. 19, 77), and memory storage of verbal information has been localized in the parietal and temporal lobes (Penfield & Roberts, 1959). Neandertals may have possessed a large brain at least partly due to the need to efficiently store potentially ambiguous verbal data. While by no means definitive, there is evidence, in fact, of disproportionately larger temporal and parietal lobes, in comparison with modern humans, in neandertal endocasts (von Bonin, 1963, pp. 34, 56–57).

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G. F. De Stefano
D. Formenti

*Institute of Anthropology,
Department of Histology
and Embriology,
University of Pavia, Italy*

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First Data on the Nuclear DNA Content (Feulgen-positive Material) of *Perodicticus potto*

The nuclear DNA content (Feulgen-positive material) of *Perodicticus potto*, measured on lymphocytes from six animals of the subspecies *edwardsi* (Gabon) and *potto* (Dahomey and Liberia) is quite homogeneous around a mean value of 6.87 ± 0.15 pg. A difference of 1.5% has been found between sexes in each subspecies; the possible relation of this fact to the characteristics of the karyotype is discussed.

1. Introduction

The nuclear DNA content (cytrophotometrically measured as Feulgen-positive material in lymphocytes of peripheral blood) is considered useful for the understanding of some cytotaxonomical problems, above all when this datum together with other characteristics of the karyotype (number and shape of chromosomes) (Manfredi Romanini, 1972, 1973) are used.

Meanwhile Jones (1973) and De Boer (1973) proved the existence of a chromosomal polymorphism among animals of the same species from different geographic regions, and stressed the need to work on a great number of individuals. Recently some variability was also observed in the nuclear DNA content, between different individuals of *Cercopithecus aethiops* (Formenti, 1973).

Concerning prosimians, only fragmentary data about Lorisidae are available in the literature. The better known species of this family seems to be *Perodicticus potto* with 62 chromosomes (Chu & Bender, 1961); this number is equal to that of *Loris tardigradus*, and greater than that of the other known Lorisidae (*Nicticebus* and *Arctocebus*) for which a number of 50–52 chromosomes was described (Chiarelli, 1973). Egozcue (1969) described the karyotype: 24 little metacentric or submetacentric, 36 acrocentric chromosomes, and a large submetacentric X and a little Y acrocentric.

2. Materials and Methods

As in previous research (Manfredi Romanini, 1972) the determination of the nuclear DNA content was made on lymphocytes of peripheral blood, considered a good model of cell population in the G_1 phase. Lymphocytes of six specimens of *Perodicticus potto* from three different countries* were studied (2 smears for each individual; 25 lymphocytes for each smear) with a Vickers M86 Microdensitometer (optic: oc. $10\times$, ob. $100\times$) at 550 nm after staining with the Feulgen reaction according to Itikawa and Ogura (1954).† As controls, two smears of human blood were simultaneously prepared and subjected to the same Feulgen reaction.

* We thank Prof. Goffart of the University of Liège, who furnished the smears.

† Fixation: 10% formalin for 20', room temperature; hydrolysis: 5N HCl for 60', r.t.; Schiff leucofuchsin in accord to Lillie, 45', r.t.).

3. Results and Discussion

Table 1 shows the results obtained and the statistically significant differences observed between different populations, between subspecies irrespective of their origin and between Man and *Perodicticus potto* specimens as a whole; a statistical comparison between males and females of the same subspecies and between subspecies is also reported.

Generally the nuclear DNA value of *Perodicticus potto* is lower than Man's value, and, accepting for the latter the absolute value of 7.3 pg proposed by Bachmann (1972), would have an absolute value of 6.87 pg.

Table 1

Species	Sex	Prov.	DNA $\pm$ s.s. (a.u.)		
<i>Perodicticus potto edwardsi</i>	m	Gabon	35.67 $\pm$ 0.72		
			35.89 $\pm$ 0.81		
<i>Perodicticus potto edwardsi</i>	f	Gabon	35.12 $\pm$ 0.83		
<i>Perodicticus potto potto</i>	f	Liberia	35.66 $\pm$ 0.57	(-)	35.90 $\pm$ 0.82
<i>Perodicticus potto potto</i>	m	Liberia	35.41 $\pm$ 0.73		
			35.91 $\pm$ 0.83		
<i>Perodicticus potto potto</i>	f	Dahomey	36.44 $\pm$ 0.77		(+)
<i>Perodicticus potto potto</i>	f	Dahomey	36.12 $\pm$ 0.84		
<i>Homo sapiens</i>	m		38.12 $\pm$ 0.73		
		<i>P.p. edwardsi</i>	<i>P. potto potto</i>	<i>P. potto</i>	
Sex		Gabon	Liberia	Dahomey	
m		35.67	(-) 35.41	35.54	
		(+)	(-)	(+)	
f		36.12	(+) 35.66	(+)	36.08
			(-)		

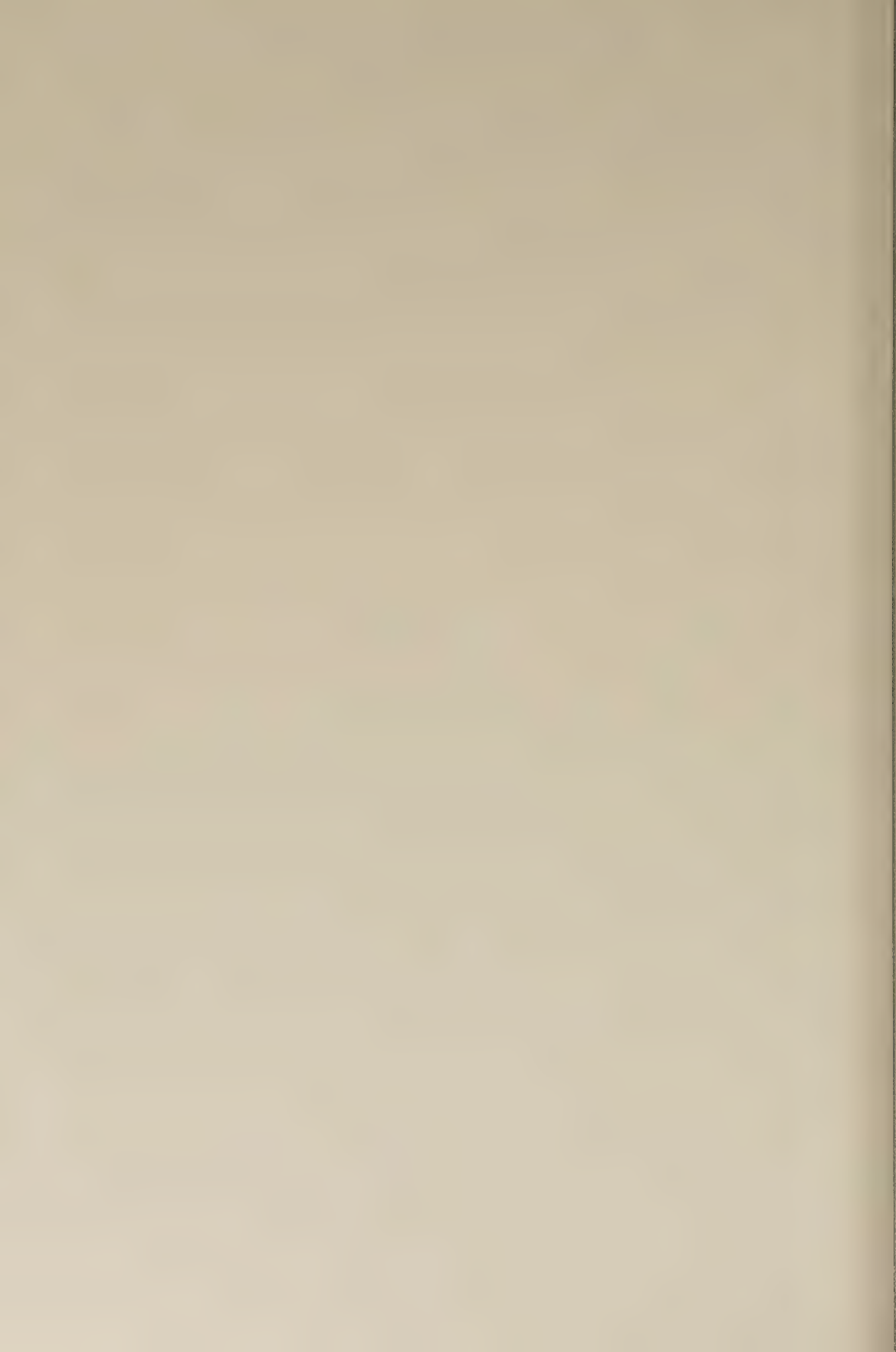
As a first approach to the problem of variability between populations from different geographic regions and between subspecies (allowance being made for the tendency to limit taxonomical subdivisions) the present data seem to show a great constancy of the nuclear DNA content; moreover it is quite interesting to observe that there is a significant difference between males and females; in the males of the two subspecies there is less DNA content than in the females (1.25% less in the *edwardsi* and 1.83% less in the *potto*). This datum, the first in the comparison between sexes in the prosimians, can be regarded as a confirmation of the characteristics of the chromosomes of *Perodicticus potto* in which all the autosomes are quite small as compared to the great X chromosomes.

Obviously, further observations on a greater number of individuals, males and females, are needed to confirm the results obtained. Should in fact the little difference observed actually be proved, it would be evident above all that the degree of sensitivity to the method employed is higher than the level of 5% of error that until now has been considered as an acceptable instrumental limit.

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K. C. Malhotra*

*RTS, Indian Statistical Institute,
Calcutta-35, India*

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accepted 10 February 1974

Absence of Attached Ear Lobes in Four Mendelian Isolates

Incidence and genetics of ear lobe type is reported among four endogamous groups from Maharashtra, India. All the 1367 subjects (682 males, 685 females) studied, showed free ear lobe type. The complete absence of attached ear lobe among the Nandiwallas is a unique finding—no other reported population in the world has shown absence of this phenotype. In 140 families of the mating type free $\times$ free, all 545 children had free ear lobes. It appears that the genetic factor for attached ear lobe has been lost in these groups due largely to genetic drift.

1. Introduction

Although a number of studies have attempted to elucidate the mode of inheritance of ear lobe attachment, none of the hypotheses presented offers an adequate explanation. Hilden (1922), Powell & Whitney (1937) and Winchester (1960) hypothesised that free ear lobe is an autosomal dominant. Weiner (1937) and Lai & Walsh (1966) have suggested that the ear lobe attachment does not follow simple Mendelian inheritance and appear to be polygenic. McKusick (1971) lists this trait as a dominant (item n. 12890). Striking variations in the incidence of this trait have been reported by several workers (Dutta & Ganguly, 1965; Lai & Walsh, 1966; Chattopadhyay, 1968; Singh & Malhotra, 1969, etc).

In the present paper (1) we report the incidence of ear lobe type among four nomadic Mendelian isolates; (2) examine the genetics of this trait; and (3) discuss the present findings in the light of possible evolutionary processes, particularly genetic drift and founder effect.

The Nandiwallas are divided into four strictly endogamous groups: Patils, Chaugule, Komti and Daundiwal. The traditional occupation of the Nandiwallas is to train bulls to perform certain tricks; they are true nomads and operate largely in Western Maharashtra, assembling once in three years at Wadapuri village in Poona district. All the four groups prefer both types of cross-cousin and uncle-niece marriage.

2. Methods and Materials

In all 1367 subjects (682 males and 685 females) from new borns to 90 year olds in 140 families and 542 unrelated persons were examined for ear lobe types: attached lobes (see Figure 907, Martin & Saller 1961) and free lobes (Table 1).

3. Results

None of the 1367 subjects observed for this variation showed attached ear lobes, and the family data are compatible with the absence of the gene for attached lobes (Table 1).

*Present address: Deccan College, Poona-6, India

Table 1 Free ear lobes among Nandiwallas

Group	Population size	Families examined	Children with free ear lobes			Total number with free ear lobes		
			Male	Female	Total	Male	Female	Total
Patil Putta	800	46	114	90	204	231	219	450
Chaugule Putta	1150	50	97	98	195	276	273	549
Komti Putta	460	40	59	72	131	160	180	340
Daundiwalla	55	4	7	8	15	15	13	28
Total	2465	140	277	268	545	682	685	1367

4. Discussion

Our finding that the factor for attached lobe is absent among the Nandiwallas is highly significant. Although the frequency of attached lobes varies considerably in Indian populations from 12 % (Tharus) (Basu, 1966) to 81 % (Devrukhe Brahmins), (Malhotra, 1966), not even a single Indian or non-Indian population is known to lack this phenotype. Since in our data more than 55 % of the entire Nandiwalla population has been sampled, we strongly feel that the attached lobes, if at all they are present, must be of very low magnitude. Our contention that the gene for the attached lobe is absent, is further strengthened due to the fact that in spite of rather high rate of inbreeding, (and if the attached lobes are due to recessive factors, as indicated by some workers) none of the matings produced even a single child with attached lobes.

It may be noted that the Nandiwallas not only differ from the other neighbouring population with respect to ear lobe types but depict striking differences in other characters also, *viz.* the Nandiwallas record lowest value of gene p_1 and Hp_1 , not only in Maharashtra but in the Indian sub-continent; they possess rather high Rh (—)—15 %—the usual incidence in Maharashtrian populations is 3–7 %, and also lack the gene p_2 and Hp^0 . They are characterized by rather low frequency of whorls on the fingers—the Komtis and Chaugules record the lowest in the Indian sub-continent—and interestingly enough Patils, Komtis and Daudinwallas also lacked gene for colour blindness. For details see Malhotra (in press). In short, although morphologically—stature, C.I., F.I., skin colour etc.—the Nandiwallas conform to the racial type called “Mediterranean” (predominantly found in Maharashtra and elsewhere in India), no other reported “Mediterranean” population has yielded such gene frequencies. In other words if the peculiarities depicted by the Nandiwallas are not due to different racial affiliations then what could be the possible explanation for these unique frequencies?

The very small effective size of these populations—Patils (240), Chaugules (345), Komtis (138) and Daundiwalla (16)—30 % of the total population size has been considered as breeding population, after Salzano & Freire-Maia (1970:106)—suggest that the obtained frequencies for various markers, including ear lobe types, are due largely to genetic drift; the possible influence of natural selection and founder effect cannot, however be completely ruled out.

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Editorial Note

As guest editors of this special issue of the *Journal of Human Evolution*, we have sought manuscripts that will serve to define some of the ways in which comparative behavioral primatological studies are contributing to our understanding of Primate evolution in general and human evolution in particular. To this end, the papers of this special issue are representative, but by no means exhaustive. This particular collection, however, should serve to inform scientists of many disciplines of some of the contributions of behaviorists to the topic of human evolution.

We hope that the readers will enjoy and benefit from the research and discussions on topics that range from the basic psychological processes to communication, tool use, and social behavior. Many authors have taken the occasion of this issue to release new important data as well as an opportunity to synthesize thought and data.

We are particularly honored that Austin H. Riesen has contributed his thoughts and perspectives regarding ways in which comparative behavioral primatology is making its impact upon science.

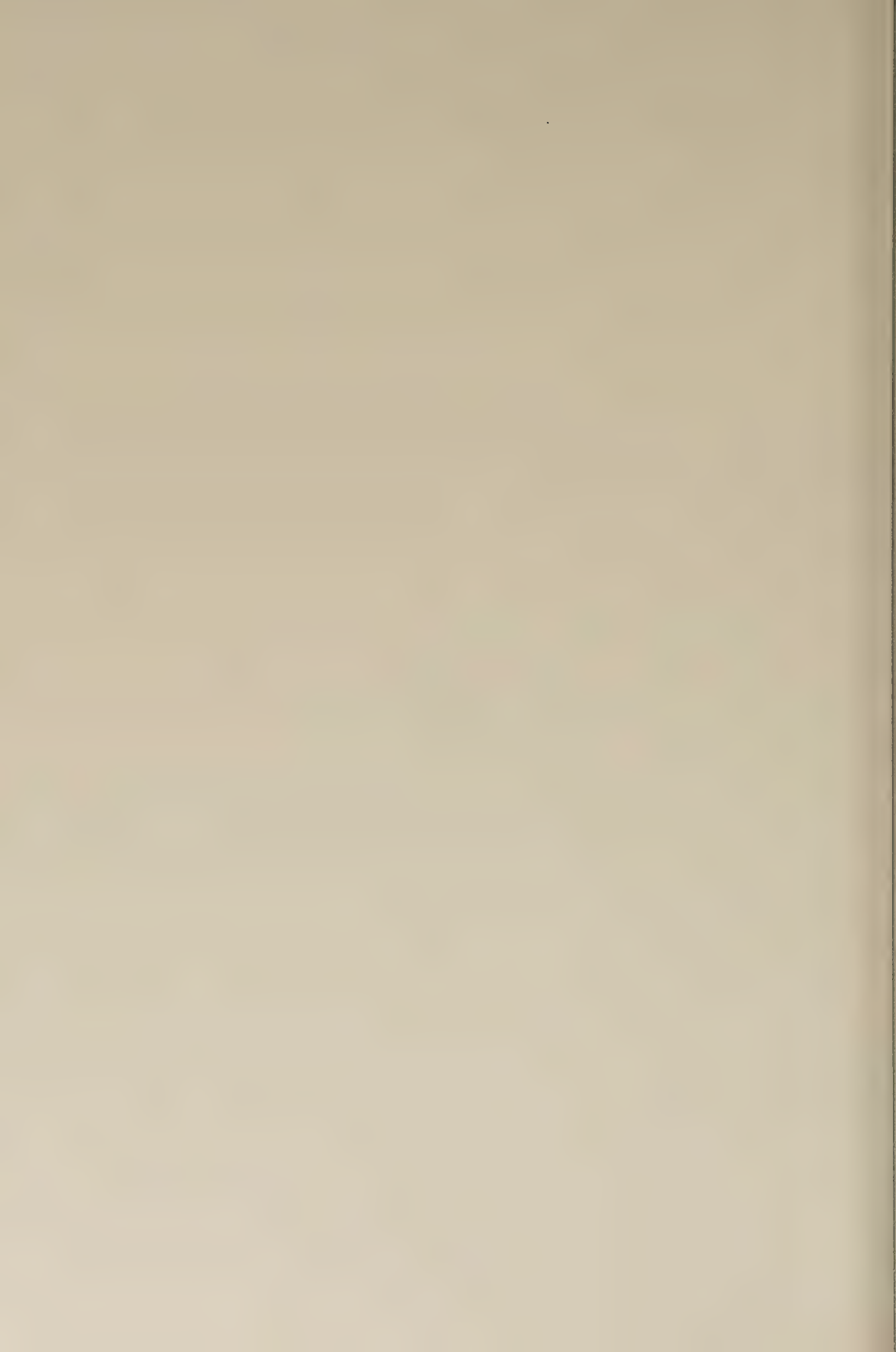
We also thank the Journal editor, Brunetto Chiarelli, for extending us the invitation to edit this special issue. We view the invitation as a rare privilege, and are hopeful that we and the authors of the papers have in no way left his aspirations for this issue unfulfilled.

*Professor and Chairman, Department of Psychology,
Georgia State University,
Atlanta, Georgia, U.S.A.
and
Yerkes Primate Research Center,
Emory University, Atlanta, Georgia, U.S.A.*

DUANE M. RUMBAUGH

*Primate Behavior Laboratory,
Department of Psychiatry,
Downstate Medical Center,
Brooklyn, New York, U.S.A.*

LEONARD A. ROSENBLUM



Austin H. Riesen

*Department of Psychology,
University of California, Riverside,
Riverside, California 92502, U.S.A.*

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accepted 12 June 1974

Comparative Perspectives in Behavior Study

Studies of behavior require preselection of criteria and rejections of irrelevant or trivial elements. Judgments based on comparative perspectives must enter heavily into this preselection process. Formal requirements for doing these important preliminary steps or at least making them explicit after the fact may one day become necessary. At present they would be undesirable. Recent demands for more restrictive definitions of comparative psychology and reactions to such demands speak to the state of the art and to the need for continuing the search for descriptive categories and behavioral principles from a broadly comparative point of view.

Behavioral development of human beings, individually and in groups, is better understood today than ever in the past. This may be ascribed in large measure to the contributions of workers whose viewpoints and research maintain a comparative perspective. Neither individual nor collective behavior can be studied adequately from the narrower approach of the anthropocentric psychologist or the historian who focuses exclusively on human accomplishments and failures. Current developmental psychology is generous in its acknowledgments and in the use of contributions from comparative behavioral research. The recent expansion of concepts and principles that enliven and challenge the field of developmental psychology stems largely from contributions of ethologists and other behavioral scientists who have taken a broader subject matter than the behavior of any single species.

Anthropologists, sociologists, and physiological psychologists are participating in the production and use of knowledge about behavior that is gained by the comparative approach. Fields are merging into each other such that no longer can boundaries be defined except in the broadest of terms. Psychobiology and biosociology are labels to be seen increasingly and represent only two of many compound names for categorizing research or instructional areas with claims for effective use of comparative behavior study. Proposals have been made to narrow the definition of comparative psychology, but such attempts do not succeed in describing or defining the real world of behavior research. The inadequacy of restrictive definitions is extensively documented in a recent volume edited by Tobach, Adler & Adler (1973), whose contents speak eloquently to the boundless energy of current comparative behavioral research.

Some have argued that only those studies involving two or more species in the same set of observations are comparative. Others insist that a tightly drawn evolutionary theory is essential in any comparative study. Such restrictions are too artificial. They stultify rather than encourage the sciences of behavior.

One's assumptions about behavioral genetics, about natural selection, or about a possible unitary theory of learning need have no critical relations to experimental or field observations. Discussion sections of research papers are appropriate places for statements about interpretations and biases, but discussions are expendable in the long range accrual of knowledge. Good data will have lasting value in spite of, not as a consequence of, good or bad discussion sections.

All behavior is dependent upon developmental processes. These will most often reflect

both genetic influences and learning, broadly defined. Comparative perspectives enter into the understanding of behavior at any age. Adult social behaviors are no exception. The treatment of their infants by monkey mothers whose own early months of life were spent in the company of unresponsive monkey surrogates (Arling & Harlow, 1967) generates questions and insights about violent behaviors in human adults. This set of observations is a contribution to comparative behavior study without being immediately associated with a human rearing experiment employing the same surrogates.

The development of affiliative patterns depends on processes whose generality is apparent across a large number of species from birds to Man. We need not have exposed representatives of each of these species in identical natural or experimental environments to learn some of these dependencies. Purists who insist that we should be entitled to retain doubts about just how equivalent across species the avoidance of strangers and the preference for the familiar companion are.

When some mechanism, environmental factor, or pre-condition is relatively weak in its effect in one species we are reminded of it or it may be forcefully brought to our attention through observations of another animal form. Phenomena like imprinting or critical periods in socialization are being studied in Primates (including Man) because of their dramatic significance for the development of behavior in other mammals and birds. Anatomical changes and behavioral correlates of early sensory deprivation have been found in lesser degree, perhaps, but with great significance for neuropsychological development in several species as a consequence of work with chimpanzees (Chow, Riesen & Newell, 1957; Riesen, 1958) and with cats (Dews & Wiesel, 1970). This area of investigation—the behavioral and the neuroanatomical studies of sensory deprivation (Riesen, 1974)—is beginning to stumble into profound differences among Primates, cats, and rabbits (Mize & Murphy, 1973). The differences are obvious even without simultaneous observations on two or more species.

Comparative physiological psychology has a long and exciting future. It is also well on its way (Pfaffman, 1973), but needs to increase its probing into the details of inter-species differences. Too much physiological psychology and even more experimental psychology of learning and motivation have been carried out under an assumption of commonalities across species. Comparative perspectives are forcing the critical re-evaluation of this assumption.

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James E. King
James L. Fobes

*Department of Psychology,
University of Arizona,
Tucson, Arizona, U.S.A.*

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Evolutionary Changes in Primate Sensory Capacities

This paper is a review of laboratory research on sensory capacities in Primates with emphasis on evolutionary changes in the capacities. Man, great apes and Old World monkeys have virtually identical color vision, a result consistent with the generalization that these relatively diverse species have reached a plateau in the evolution of color vision. Capuchin and squirrel monkeys are protonomalous trichromats thus suggesting a widespread relative insensitivity to red among New World monkeys. Of the prosimians, only tree shrews have been extensively tested for color vision capability and they are deuteranopic dichromats.

There is clear evidence of a decline in the upper audible frequencies and the most audible frequencies during Primate evolution. Although the olfactory portion of the brain has declined markedly in relative size during Primate evolution, there is no corresponding research showing difference in olfactory sensitivity across the living Primate genera. Existing research on gustatory sensitivity in Primates is too limited to permit any evolutionary conclusions.

Basic changes in sensory mechanisms and capacities occurred as insectivores evolved into Primates during the late Cretaceous period. These changes included rapid elaboration of vision manifested by development of color vision and increased orbital frontality, concomitant reduction of reliance upon olfaction and major frequency shifts in auditory sensitivity. Clearly, defined hypotheses concerning specifics of evolutionary changes in sensory mechanisms must depend upon careful, detailed study of sensory capacities of living Primate genera. Therefore, the purpose of this paper is to review the literature relating to differences in sensory capabilities among Primates and, where possible, to indicate how these differences relate to theories of the sensory evolution of Primates.

1. Methodology

Two fundamental behavioral techniques exist for categorizing interspecies differences in sensory functioning. One entails comparisons of subjects' relative responsiveness to stimuli which vary along some dimension. Visual spectral sensitivity curves and auditory threshold functions are examples of such relative comparisons. The other technique involves comparisons of absolute sensitivity to a constant stimulus.

When a subject's sensitivity to a stimulus is inferred from a learned discrimination, it is important to recognize that nonsensory response biases such as position habits, position alternation and tendencies to choose a previously rewarded position may lower overall performance as measured by percentage of correct responses (Levine, 1959). Subjects' theoretical sensitivity parameters as defined by a signal detection theory (e.g. d') are assumed to be independent of position habits (Green & Swets, 1966) and other of the above biases (King & Fobes, 1973). However, highly trained capuchin monkeys manifest increased position responding if the difficulty of a two alternative forced choice brightness discrimination is sufficiently increased (King & Fobes, 1973). Thus, extensive pretraining does not ensure elimination of response biases when the discrimination is difficult. If one species manifests a greater increase in response biases than another as difficulty is increased equally for both, interspecies sensitivity differences based on percentage of correct

responses will be misleading since the former species will indicate a spuriously low sensitivity. Although the literature on interspecies differences in response biases is meager, there is justification for expecting marked interspecies differences in susceptibility to response biases. For example, capuchin and squirrel monkeys probably have stronger propensities for position habits than do rhesus monkeys (see King & Fobes, 1975). While a forced choice discrimination procedure minimizes response biases in humans (Green & Swets, 1966) it clearly does not for those nonhuman Primates that manifest strong position habits.

In our review of Primate sensory literature we did not find any study on interspecies differences incorporating a sensitivity measure which was based on signal detection theory and therefore relatively independent of response biases. Without use of a signal detection analysis, response biases will obviously exert a strong confounding influence on comparisons of absolute sensitivity but should have less effect on relative measures, especially points of maximum and minimum sensitivity. Therefore, this review will be directed mainly toward the latter types of measures.

2. Vision

Spectral sensitivity

Spectral sensitivity or luminosity curves are measures of subjects' sensitivity to different spectral frequencies and, for Primates with a duplex retina, these functions differ with scotopic (dim light) and photopic (bright light) conditions. Determinations of sensitivity curves in nonhuman Primates have frequently been made by plotting either absolute thresholds or fusion frequency (CFF) of a rapidly flickering light as a function of wavelength.

To date, no scotopic sensitivity curves have been determined for any of the apes. Grether (1940c) found that spectral limits of photopic sensitivity in three chimpanzees were about the same as those in humans. However, he did not determine a complete sensitivity curve. Blough & Schrier (1963) obtained scotopic sensitivity curves for rhesus monkeys trained to press levers in order to maintain monochromatic stimulation at threshold visibility. DeValois *et al.* (1974) reported similar curves for three macaque species based on the flicker technique. Both of the above functions were virtually identical to the human scotopic curve (Commission Internationale de l'Eclairage) with maximum sensitivity at 510 nm. Adams & Jones (1967) similarly found that scotopic sensitivity curves for mangabey monkeys were similar to those for humans.

Photopic sensitivity curves for macaque species have been obtained with the threshold tracking procedure (Blough & Schrier, 1963), a threshold food reward discrimination (Grether, 1939), the flicker technique (DeValois *et al.*, 1974), and shock avoidance wherein threshold monochromatic light was a CS (Sidley *et al.*, 1965). Some differences occurred depending upon procedure, but human and macaque curves were similar with a maximum sensitivity at 550 nm whenever the same procedures were used. The main difference was that compared to human observers, macaques had slightly increased sensitivity for short wavelengths relative to long wavelengths. Adams & Jones (1967) also reported a similar enhanced relative sensitivity to short wavelengths in photopic sensitivity curves of mangabey monkeys.

Scotopic and photopic visibility curves for capuchin and squirrel monkeys based on flicker thresholds have points of maximum sensitivity comparable to those from human

observers (Jacobs, 1963; DeValois, 1965; DeValois & Jacobs, 1971). Capuchin monkeys possibly have a slight relative decrease in photopic sensitivity for wavelengths longer than 600 nm while squirrel monkeys have considerably greater relative loss in photopic sensitivity for longer wavelengths.

A scotopic sensitivity curve for a galago tested by Silver (1966) with a threshold discrimination procedure showed a maximum at 518 nm, somewhat above the comparable maximum for humans and macaques. This obtained sensitivity curve was closely predicted by a model developed by Dartnall *et al.* (1965) which allowed for fluorescence of the tapetum in all rod retina of the galago. In contrast, tree shrews possess a virtually all cone retina and therefore only a photopic sensitivity curve can be obtained from these extremely primitive Primates. Polson (1968) showed that their photopic function was similar to that from humans except for a slight relative loss at both long and short wavelengths.

Color vision

Several different tests of color vision capabilities have been applied to Primates where a basic test is examination of a subject's ability to discriminate between monochromatic stimuli on the basis of hue differences. Another technique is a neutral point test for the existence of a monochromatic hue which cannot be discriminated from white when brightnesses of the two stimuli are equated; trichromats have no neutral point but all dichromats do. An additional procedure is the anomaloscope test which determines the proportions of two wavelengths, usually red and green, in a mixture which cannot be discriminated from a single monochromatic wavelength, usually yellow. This test measures relative sensitivity to red and green and is an important technique for quantifying the degree of defect in protanomalous and deuteranomalous trichromats. Finally, saturation tests are used to measure the amount of monochromatic light at different wavelengths which must be added to white in order that the combination be discriminable from white.

Grether (1940*a,d*) found that the function relating chimpanzees' difference thresholds for hue discriminations to wavelengths was similar to that of human observers he also tested. Anomaloscope matches (Grether, 1940*b*) for chimpanzees and humans were virtually identical as were saturation curves which showed minimum saturation at 570 nm for chimpanzees and at 575 nm for humans.

Similarly, DeValois and his co-workers (DeValois & Jacobs, 1971; DeValois *et al.*, 1974) demonstrated that macaques have hue discrimination functions, anomaloscope match values and saturation curves similar to those for humans. No evidence of a neutral point was found. Clearly, chimpanzees' and macaques' color vision mechanisms closely approximate those of the normal human trichromat.

Of the New World monkeys, only capuchin and squirrel monkeys have been extensively examined on color vision tests. Both species have greater difficulty discriminating hue differences among long than among short wavelengths and the defect is considerably more exaggerated in squirrel monkeys than in capuchin monkeys (DeValois & Jacobs, 1971; DeValois & Morgan, 1974). While neither species has a neutral point, both have considerable difficulty discriminating wavelengths of 480–510 nm from white (Jacobs, 1963; DeValois & Jacobs, 1971). Finally, anomaloscope tests indicated that both species require more red or orange in a mixture with green to match yellow or white than do

normal trichromats (Grether, 1939; Jacobs, 1963). These results in addition to previously discussed low photopic sensitivity to long wavelengths are strong evidence that both species are protanomalous trichromats with squirrel monkeys probably being more anomalous than capuchin monkeys.

Surprisingly little research on the color vision of prosimians has been reported, an unfortunate lack in view of the importance of this group in understanding the beginnings of Primate evolution. Glickman *et al.* (1965) presented evidence that a lemur was able to learn a red-blue discrimination on the basis of hue differences but no further tests were made. Polson (1968) made a thorough study of color vision in tree shrews. These primitive Primates have a neutral point at 505 nm similar to that of human deuterans and tree shrews cannot discriminate among hues on the same side of their neutral point. Furthermore, their hue discrimination function has a break near the neutral point similar to that characteristic of human protans and deuterans. Isochromatic match tests showed tree shrews cannot discriminate extraspectral purples from blue, green or yellow and provided conclusive evidence that tree shrews are deuteranopic dichromats. Tree shrews are the only mammals yet shown to be typically dichromatic deuteranopes by behavioral techniques.

Evolution of color vision

The original mammals evolved from diurnal reptiles during the Jurassic period and rapidly became nocturnal as a result of pressures from large diurnal reptiles. After reptiles' decline during the Cretaceous period, mammals rapidly radiated, but most retained some degree of nocturnality and correspondingly poor color vision. In contrast, Primates quickly became predominantly diurnal and acquired excellent color vision. The nocturnality of some prosimians is probably a secondary adaptation (Walls, 1942; Polyak, 1957). Color vision has been demonstrated in several non-Primate mammals such as cats, tree squirrels and prairie dogs (Meyer & Anderson, 1966; Cain & Carlson, 1968; Michels & Schumacher, 1968), but it is probably poorer than that of most Primates.

Polyak (1957) speculated that rapid development of color vision in Primates during the Cretaceous and Paleocene times was enhanced by concurrent evolutionary development of colored fruits in tropical forests inhabited by early Primates. Color vision presumably aided these Primates in discriminating ripe from unripe fruit or dense green foliage. We suspect that this imaginative and intriguing theory is more colorful than scientifically fruitful.

The existence of color vision in tree shrews and probably in diurnal lemurs indicates that color vision appeared early in Primate evolution and later evolved into the trichromatic variety. The protanomalous defect in squirrel and capuchin monkeys suggests that this anomaly may be fairly pervasive in New World Primates. Moreover, the relatively mild deficit in capuchin monkeys suggests that the more evolved New World Primates such as capuchin, spider and woolly monkeys may have a less severe deficit than less evolved forms such as squirrel monkeys and marmosets. However, this possibility is speculative and more species need to be tested before a definite conclusion can be made.

Finally, the similarity in color vision capacities of humans, chimpanzees and macaques is striking since these species represent three fairly divergent groups among Old World anthropoids. It appears likely that Old World anthropoids have reached a plateau in color vision development and that little change occurred in recent evolutionary history.

3. Olfaction

Prosimians possess a highly developed olfactory sense which facilitates environmental exploration as well as social communication based on chemicals in urine, feces or specialized scent glands (Petter, 1965; Ralls, 1971). Prosimian scent marking is frequently accompanied by extensive repertoires of ritualized marking behaviors (Jolly, 1966). Olfactory communication investigated in the laboratory indicated its importance in territoriality, orientation, identity and sexual status (Seitz, 1969; Harrington, 1972).

As Primates evolved, olfaction probably became progressively less acute while vision became more acute. Gland marking and ritualized behavior involving urination and defecation is less common in anthropoids than in prosimians. Decreasing reliance upon olfaction as a dominant mode of communication was accompanied by changes in olfactory anatomical correlates; nasal passage structure and relative olfactory brain volume have undergone considerable change (Marler, 1965). The olfactory brain proportion of total brain volume has decreased from 0.01 in prosimians (20 species), to 0.001 in monkeys (18 species), to 0.0008 in great apes (2 species) to 0.00009 in Man. The olfactory proportions of telencephalon volumes for these groups are 0.02, 0.001, 0.007 and 0.0001 (Stephan *et al.*, 1970). Thus, the relative telencephalon volume for olfaction in prosimians is 20 times greater than in monkeys, 25 times greater than in apes and 200 times greater than in humans.

4. Audition

Minimal intensity thresholds across a range of audible frequencies presented are available for a variety of species although these thresholds are based on learned responses established by a variety of positive and negative reinforcers and experimental techniques. Shock avoidance, conditioned suppression and food reward techniques all result in similar sensitivity estimates for anthropoids (Stebbins, 1971). However, for prosimians, shock avoidance results in lower thresholds than food reward (Mitchell *et al.*, 1970, 1971). Various summary characteristics of audiograms that have been estimated from published figures are presented in Table 1.

High frequency cutoff and best frequency

Hominoidea's high frequency cutoff is strikingly low relative to other mammals. Sensitivity above 32 kHz has been reported for 17 of 19 mammals examined and this primitive and uniquely mammalian characteristic is thought to have resulted from selective pressure for localization of sound sources by species with closely set ears (Masterton, Heffner & Ravizza, 1969). These investigators noted an inverse relationship between high frequency cutoff and availability of time cues for sound localization; high upper limits are associated with reduced maximal binaural time disparity cues which accompany closely set ears. Therefore, primitive Primates probably relied on binaural intensity disparities for localization since even small heads can induce intensity disparity with high frequencies. As the distance between ears lengthened during the Eocene epoch, temporal sound disparity increased and selective pressures for high frequency sensitivity lessened.

Complete information on high frequency sensitivity includes differential frequency discrimination ability. Weber fractions ($\Delta F/F$) at 30–40 dB above threshold are available

Table 1 Summary characteristics of audiograms

Taxa	Low		Low Frequency Sensitivity (dB)			Best		High		Source
	kHz	dB	0.25	0.5	1(kHz)	kHz	dB	kHz	dB	
Tree Shrew	0.250	55	55	27	30	16	-10	60	58	Heffner <i>et al.</i> (1969a)
Lemur	0.100	49	33	19	7	8	3	75	86	Mitchell <i>et al.</i> (1971); Gillette <i>et al.</i> (1973)
Loris	0.063	67	36	30	24	16	9	48	69	Heffner & Masterton (1970)
Potto	0.125	64	33	31	18	12	-2	43	70	Heffner & Masterton (1970)
Galago	0.250	43	43	25	28	8	5	60	55	Heffner <i>et al.</i> (1969b)
Marmoset	0.100	42	27	12	4	8	-9	35		Seiden (1958)
Owl Monkey	0.125	39	23	13	6	10	-8	46	70	
Squirrel Monkey	0.063	39	17	2	5	10	-4	46	70	Fujita & Elliot (1965); Beecher (1974)
Spider Monkey	0.064					1				Wendt (1934)
Capuchin				13	15					Dalton (1968)
Macaque	0.063	32	16	8	3	1	3	45	82	Stebbins <i>et al.</i> (1966)
Mangabey	0.064					2.1				Wendt (1934)
Baboon	0.064					2.1				Wendt (1934)
Chimpanzee	0.128	30	19	9	1	2	-2	24.5	80	Elder (1934); Farrer & Prim (1965)
Human	0.060	43	16	8	0	3	-7	20.6	80	Sivian & White (1933); Farrer & Prim (1965)

dB re 0.0002 dyne/cm².

for several Primate species and although their entire range was not tested, nonhuman Primates were able to discriminate between frequencies well above human upper limits. Weber fractions varied from 0.02 to 0.45 across 0.5 to 42 kHz for tree shrews (Heffner, Ravizza & Masterton, 1969a), galago fractions varied from 0.007 to 0.02 across 0.5 to 32 kHz (Heffner, Ravizza & Masterton, 1969b), those of macaques varied from 0.008 to 0.017 across 0.5 to 30 kHz (Stebbins, Pearson & Moody, 1970), and Man's varied from 0.002 to 0.006 across 0.5 to 12 kHz (Geldard, 1953). In addition to demonstrating that nonhuman Primates are able to discriminate among frequencies well above the human range, the consistency of the Weber fractions is evidence against the existence of an unusual mechanism for high frequency hearing by Primate species sensitive to very high frequencies (Heffner, Ravizza & Masterton, 1969b).

Best frequencies (i.e. those which require the lowest intensity to be detectable) have been considerably reduced during Primate evolution. While some overlap exists between prosimians and monkeys, both groups are maximally sensitive to frequencies that are generally one to two octaves above man's best frequency.

Low frequency sensitivity

Low frequency sensitivity indicated by minimal detectability intensities for 0.25, 0.5 and 1 kHz has increased considerably during Primate evolution; sensitivity to low frequencies is not a primitive Primate characteristic. Mitchell, Vernon & Herman (1971) showed that prosimians' (tree shrew, loris, potto and galago) low frequency thresholds were significantly higher than those of anthropoids (capuchin, squirrel monkey and macaque).

The increase in low frequency sensitivity is thought to have occurred slowly until the Paleocene, rapidly through the Eocene, and remained relatively unchanged until the present (Masterton, Heffner & Ravizza, 1969). Thus, increased sensitivity to low frequencies resulted in progressive increases in the size of audible fields in man's lineage. However, since the Eocene, the area of audible fields has decreased due to reduction in high frequency sensitivity.

5. Taste

Concentrations at which sucrose or saccharin (sweet), quinine hydrochloride (bitter), sodium chloride (salty) and acetic acid (sour) are differentially chosen have been determined for tree shrews, lorises, galagos, marmosets, tamarins, squirrel monkeys, macaques, chimpanzees and humans (Patton & Ruch, 1944; Skramlik, 1948; Weiskrantz, 1960; Fisher, Pfaffmann & Brown, 1965; Glaser, 1968, 1970, 1972). Although humans are the most sensitive to four of the five stimuli, this may be due to humans reporting initial detection concentrations rather than preference or aversion thresholds. With this reservation, no relationship can be stated regarding sensitivity and phylogenetic position.

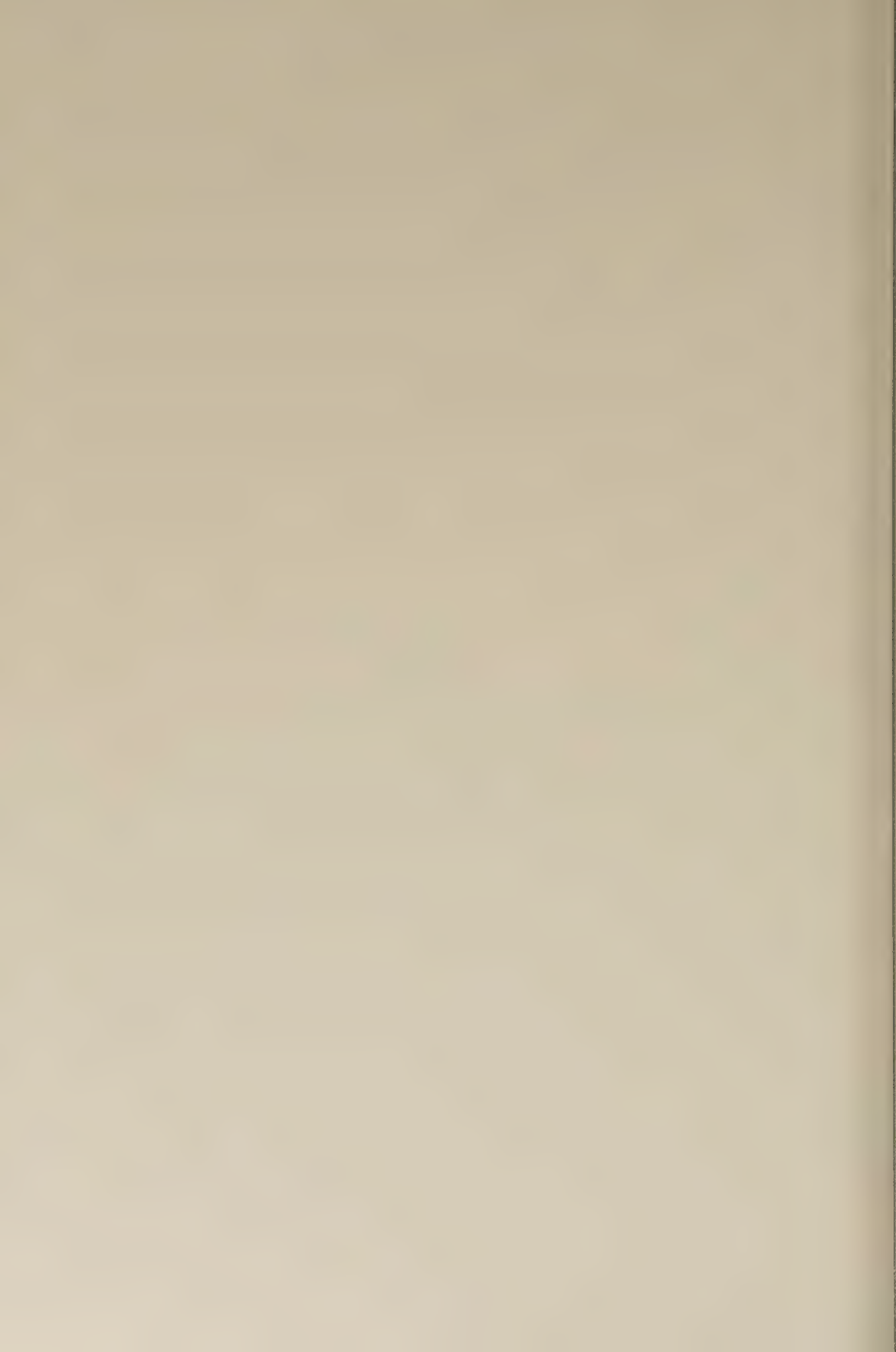
Sensitivity to phenyl-thio-carbomide (PTC), an organic substance tasting bitter to about 80% of humans and tasteless to the rest, is a manifestation of primate gustation partially having a genetic basis. Population frequencies of PTC sensitivity in Primates indicated heterozygous conditions in all 28 genera for which more than one subject was tested, except for spider and woolly monkeys (Chiarelli, 1963*a,b*; Eaton & Gavan, 1965). However, variability precludes any statement about evolutionary trends. When subjects were tested with varying concentrations, bimodal sensitivity distributions were observed in humans, chimpanzees, and gibbons (Eaton & Gavan, 1965). In other species there was either a unimodal distribution, such as in macaques, or data are too meager for conclusions.

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J. M. Warren

*Animal Behavior Laboratory,
The Pennsylvania State University,
University Park, Pennsylvania 16802,
U.S.A.*

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Possibly Unique Characteristics of Learning by Primates

The experimental literature on learning by Primate and non-Primate mammals is reviewed, with the aim of identifying peculiarly Primate features of learning. The evidence indicates that quantitative comparisons of learning by Primates and other mammals are intrinsically equivocal and uninformative because of the impossibility of equating experimental conditions for members of different species. The comparative results of early learning set studies were seriously misleading because the test conditions discriminated against representatives of species in which vision is not a dominant modality.

Analyses of transfer between different learning tasks strongly suggest that rhesus macaques differ qualitatively from non-Primates like cats in that they develop generalized, trans-situationally valid response strategies during training on a particular problem which can facilitate learning in other situations. Non-Primate mammals appear not to develop such strategies under the same circumstances. There is also evidence that monkeys are more able than cats to discard previously learned strategies when they are no longer maximally profitable.

This paper reviews the experimental literature on learning by Primate and non-Primate mammals; only those laboratory learning tasks on which representatives of both groups have been tested shall be treated here. The purpose of the review is to examine the possibility that at least some Primates possess learning capacities that are not found in other sorts of mammals. Both the evidence for quantitative differences in the rate and asymptote of learning, and the evidence for qualitative differences in the learning performances of Primate and non-Primate forms will be considered.

1. Quantitative Comparisons

The rate with which animals of a given species learn is very strongly affected by differences in a large number of experimental variables: the characteristics of the stimulus which controls the response, the nature of the response required, the level of motivation under which the subjects are trained, the quantity and quality of reinforcement provided, and characteristics of the testing apparatus and of the training procedures.

Indeed, the success or failure of attempts to teach animals a particular response often depends on fairly subtle features of the training situation. Thus, Yamaguchi & Meyers (1972) failed, in 50 sessions, to obtain any evidence that rhesus monkeys can learn selectively to vocalize in the presence of a visual cue for food rewards, and concluded that rhesus monkeys are unable to make vocal operant responses. This conclusion was quickly invalidated by Sutton *et al.* (1973), who showed that rhesus monkeys clearly learn to emit vocalizations of specified intensity and duration in the presence of a discriminative stimulus, if trained with visual feedback about the quality of the vocal responses, and punishment for incorrect responses with a time out. Yamaguchi & Meyers' (1972) failure appears therefore due to the limitations of their procedures, and not to the incapacity of rhesus monkeys for learning vocal operants.

In general, experience has convinced comparative psychologists that variations in experimental conditions are far more influential determinants of the rate with which

mammals solve simple and moderately complex learning problems than species membership. It has been agreed for many years that Primate and non-Primate mammals cannot be differentiated by the rate with which they solve such problems (Lashley, 1949; Harlow, 1958). The list of tasks which fail to reveal differences in the numerical scores of apes and monkeys versus non-Primate mammals is quite long, and includes classical and instrumental conditioning, maze learning, discrimination learning, repeated reversal and probability learning, and more complex problems like delayed response, double alternation and multiple choice (Brookshire, 1970; Warren, 1965*a,b*, 1973).

2. Learning Sets

There is one apparent exception to the rule that the learning performance of monkeys and apes cannot be differentiated quantitatively from that of other mammals. Chimpanzees and rhesus monkeys are superior to New World monkeys, who, in turn, are superior to non-Primate mammals in the rate and final level of attainment on learning set problems. Since there are still psychologists (e.g. Hodos, 1970; Jerison, 1973) who consider the results of learning set experiments important in the comparative study of learning, it seems worthwhile to evaluate the methods and results of the learning set experiments.

The learning set technique, which Harlow first described in 1949, excited considerable interest because it entails "learning to learn", the development of a generalized capacity for solving discrimination problems of the same class with progressively greater efficiency. In a learning set experiment, the subject is trained on a series of many different discrimination problems, between pairs of stimuli that typically vary in multiple sensory dimensions. Almost always the discriminanda are objects that differ in several visual characteristics, like color, shape, size, texture, etc. In each pair, one object is consistently rewarded, and the other consistently unrewarded. A single discrimination problem is presented for a fixed number of trials, or until the animal satisfies a specified criterion of learning.

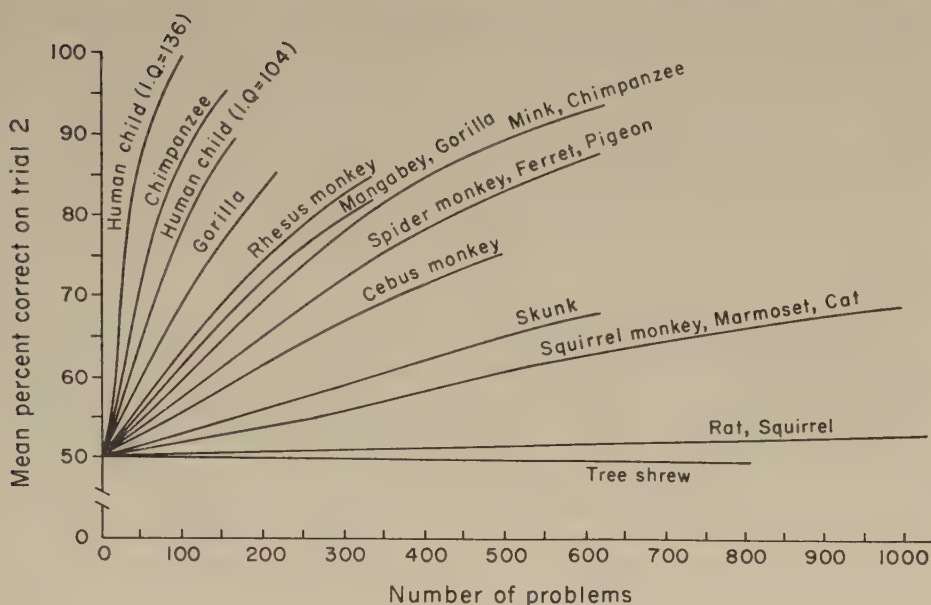
Under either procedure, rhesus monkeys show a marked change in their learning performance with continued practice. Early in training, experimentally naïve monkeys learn slowly and inefficiently, but, by the time they have been tested on 300 or 400 problems, they show essentially one-trial learning, averaging more than 95% correct responses on the second trial of each problem. (The monkeys continue to respond at chance on Trial 1 because the only cue to which object is correct in a given problem is whether or not it is reinforced on the first trial.)

The most comprehensive summary of the learning set results from mammals is provided by Hodos (1970) in Figure 1 which summarizes the findings from 16 species of mammals, tested on hundreds of visual discrimination problems. This figure reveals very large differences in the rate of learning and in terminal level of one-trial learning realized in different species.

Unfortunately, these data tell us very little of general learning ability or its phylogeny, for the same reason that other tasks providing only quantitative indices fail to do so. It is impossible to tell to what extent the results are determined by possible interspecies differences in learning capacity, or by interactions between contextual variables and interspecies differences in other characteristics.

Intraspecies analyses of learning set performance show that quantitative performance

Figure 1. Learning set formation by several species (from Hodos, 1970).



on learning set problems is just as strongly influenced by variations in multiple experimental conditions as performance on single learning problems, and, thereby, indicate that the results shown in Figure 1 are equivocal because they were obtained under "standard" conditions which were almost certainly not equally favorable for optimum learning by all the species studied. Squirrel monkeys, for example, form learning sets more rapidly and solve more problems in a single trial if they are trained to criterion (Rumbaugh & McQueeny, 1963) than if they are tested for 6 trials on every problem (Miles, 1957). Rhesus and cebus monkeys also form learning sets more quickly if trained to criterion than for 6 trials per problem (Devine, 1970). Rhesus monkeys achieve higher levels in learning set performance when trained with large rather than small reinforcements (Schrier, 1958; Schrier & Harlow, 1956). There are no data concerning the effects of incentive magnitude on learning set formation in other species, but it takes an impossible act of faith to believe that all of the species studied in comparative learning set experiments have been tested under equivalent conditions with respect to this variable.

There is much more information available concerning the influence of stimulus variables than any other potentially important determinant of learning set performance. The evidence indicates that one may obtain from rhesus monkeys almost any level of learning set performance, from near chance to almost perfect performance, by appropriate manipulation of the stimulus characteristics the subjects are required to differentiate. Objects that differ in color are more readily discriminated than the same objects with color cues eliminated (Devine, 1970). Achromatic objects are, in turn, more or less easily discriminated as a function of the number of dimensions in which they differ (Warren *et al.*, 1963). Three dimensional objects are considerably more easily discriminated by rhesus monkeys in learning set experiments than two dimensional visual patterns, squares of cardboard which differ in the characteristics of superimposed patches of construction paper (Meyer, Treichler & Meyer, 1965). A group of rhesus macaques that averaged

92% correct responses on trial 2 in object discrimination learning set performance (Harlow & Warren, 1952) were subsequently trained on a series of discrimination problems with visual patterns that differed in color, form and size. The percentage of correct responses on trial 2 was 75 on the patterns differing in color, and about 60 on the patterns that differed in form or size, considerably less than the 92% level previously realized on object discriminations (Warren, 1953c). Performance on pattern discrimination problems with stimuli varying either in color or in form was also shown to differ significantly as a function of the area of the differential cues, the monkeys attaining high performance levels when tested with larger than with smaller differential cues (Warren, 1953a,b).

There are almost no data available concerning the influence of stimulus parameters on learning formation in non-Primate species of mammals. The available data are, however, consonant with the idea that learning set performance is strongly affected by the number and conspicuity of the cues provided, just as is the case with monkeys. Cats trained with objects that differ only in visual form develop learning sets much more slowly, and attain inferior terminal levels of performance, than cats trained with objects differing in multiple visual dimensions (Warren, 1973). Rats trained on olfactory discrimination problems make more errors in forming a learning set if they are obliged to discriminate between variants of the same floral essence than if they are required to discriminate distinctly different floral essences (Slotnick & Katz, 1974).

Primates differ from other mammals in their extraordinary development of the visual system. They surpass most other mammalian species in respect to their capacity for color vision, stereopsis and visual acuity. Since, then, the visual learning set performance of monkeys varies greatly as a function of stimulus factors, it is apparent that we have no basis for guessing the degree to which the inferior performance of non-Primate species on visual learning set problems reflects an inferiority in visual sensitivity and perception instead of a defective capacity for learning.

There is now fairly compelling evidence that testing mammals other than Primates on visual learning set tasks provides a gross underestimate of their capacity for interproblem learning. The performance of a dolphin on series of visual discrimination problems can only be described as dismal by Primate standards (Herman *et al.*, 1969). Yet when a dolphin was tested on a series of auditory discriminations, under conditions as much as possible like those obtaining in learning set experiments with monkeys, it attained a final average of 86% correct responses on trial 2, a level of achievement which falls well within the range of individual differences among monkeys and apes on visual object discrimination problems (Herman & Arbeit, 1973).

Rats trained on many hundreds of six-trial visual discrimination problems display only marginal capacity for learning set formation. Very different results are observed when rats are tested with olfactory rather than visual stimuli. Four rats trained under the most favorable circumstances by Slotnick & Katz (1974), i.e. to discriminate between qualitatively different floral odors like rose and jasmine, averaged over 50 errors to criterion on their first discrimination but made only 1 or 2 errors in solving the sixteenth odor discrimination problem on which they were tested.

These findings concerning the formation of auditory and olfactory discrimination learning sets by dolphin and rats indicate that the pattern of interspecies differences shown in Figure 1 probably reveals much more about differences among species in sensitivity to visual cues than learning *per se*.

Not all methods for quantitative comparisons are necessarily unprofitable. Rumbaugh & Gill (1973) trained Primates to identical criteria on series of discrimination problems and observed their performance on sets of 10 reversal trials. They showed that the great apes were both quantitatively and qualitatively superior to gibbons, monkeys and lemurs in reversal performance after a common level of prereversal attainment. This technique of control by equation of performance should be used with non-Primates.

3. Qualitative Comparisons

The best direct evidence of differences in the quality of learning by Primates and non-Primate mammals comes from studies of intertask transfer. In these experiments, macaque monkeys are, at best, only quantitatively superior to non-Primates in initial learning of a particular task. But later transfer tests reveal striking differences in what the monkeys and non-Primates learned during original training. Three effects will be described: (1) generalization of the double alternation principle; (2) transfer from repeated reversal training to learning set problems; and (3) suppression of transfer from learning set to probability learning problems.

Generalization of double alternation

The double alternation problem is one in which the animal is confronted with two visually identical stimuli and is required to choose the right (R) and left (L) objects in RRL sequence, in the absence of useful external cues. Livesey (1965, 1969) trained representatives of several mammalian species on this task with the same procedure. He found that double alternation is not initially a congenial task for rhesus monkeys; they learned more slowly than rabbits, cats and raccoons, and at about the same rate as rats. Yet most monkeys, after learning the double alternation problem, are able to learn rather quickly to respond in double alternation sequence on sets of 8 and 12 responses (Gellermann, 1931; Livesey, 1969). Neither raccoons (Johnson, 1961) nor cats (Stewart & Warren, 1957; Yamaguchi & Warren, 1961) are able to generalize the double alternation principle successfully when tested on sequences of 8 responses. This pattern of results suggests that the monkeys, although they initially learn more slowly than cats or raccoons, have acquired a more general solution to the problem since they are able to deal successfully with sequences twice and three times the initial length. Analyses of individual responses in extended sequences strongly suggest cats and raccoons solve the four-response sequence by adapting a rule of responding twice to the right and to the left on all subsequent trials, in contrast to the monkeys' rule of alternating after every two responses to a given side.

Note that, in view of the relatively poor performance of the monkeys in initial double alternation learning, one can hardly explain their superior ability to deal with longer sequences more adequately than other species by their being tested under particularly favorable experimental conditions. It is reasonable to argue that the monkeys learned the initial double alternation task slowly because they were learning in a different way than the carnivores and lagomorphs, and that this difference is revealed by the quality of their behavior on tests for extension of double alternation responding with longer sequences.

Transfer from repeated reversal training to learning set problems

Chimpanzees (Schusterman, 1964) and macaque monkeys (Schrier, 1966; Schrier, in press; Warren, 1966) trained on repeated reversals of a single discrimination habit subsequently form discrimination learning sets more rapidly than experimentally naïve control animals. This facilitation of performance is generally attributed to the chimpanzees and monkeys developing a "win-stay, lose-shift" strategy; the animals learn more consistently to repeat reinforced choices and not to repeat nonreinforced choices during reversal training, and then apply this strategy with positive transfer effects on the learning set problems which require responses in conformity with the same rule. Two kinds of experimental evidence exclude the possibility that the facilitation of learning set performance reflects no more than simple habituation to the experimental apparatus and training procedures. Chimpanzees trained on a problem (object alternation) which militates against the development of a win-stay, lose-shift strategy do not show the facilitation in learning set performance seen in chimpanzees pretrained on reversal problems (Schusterman, 1962). And stumptailed macaques given extended training on a single visual discrimination habit, on which performance quickly becomes perfect, show no facilitation on learning set, apparently because this training does not entail frequent changes in the designation of the correct and incorrect stimuli and does not require appropriate shifts in the monkeys' choices as reversal training does (Schrier, in press).

There is one direct interspecies comparison of the effects of repeated reversal training on learning set formation (Warren, 1966). Three groups of rhesus monkeys and three groups of cats were studied. The control groups of monkeys and cats were trained to criterion on 80 visual discrimination problems without prior reversal training. The two experimental groups in each species learned 60 reversals of a single discrimination before being tested on the learning set problems; one experimental group within each species was trained on visual, and the other on spatial reversals.

The course of reversal learning was very similar in the experimental groups of monkeys and cats. The results of the learning set phase were, however, conspicuously different for the two species. Both experimental groups of monkeys made significantly fewer errors on the learning set problems than the control monkeys. Thus the monkeys trained on repeated reversals develop a win-stay, lose-shift strategy that facilitates the formation of learning sets. In contrast, no hint of transfer effects, positive or negative, was seen in the experimental groups of cats.

The findings of the experiments on double alternation and transfer from reversal to learning set problems suggest, therefore, the hypothesis that rhesus monkeys differ from cats and other non-Primate species in their ability to develop generalized, trans-situationally valid response rules during training on a specific problem, which mediate positive transfer in new test situations. To the extent that cats and other non-Primate mammals develop strategies or rules, they appear to be specific to the particular task on which they are trained, and not generalized to other situations in which the same type of strategy would be appropriate.

It is important to note that not all Primate species show positive transfer from reversal training to learning set, as macaques and chimpanzees do. Squirrel monkeys trained on 60 repeated reversals of an object discrimination task did not differ significantly from controls trained for equivalent number of trials on a single discrimination without reversals when both groups were tested on learning set problems (Ricciardi & Treichler,

1970). The major effect of reversal learning in squirrel monkeys appears to be the enhancement of adaptation to the test situation, not the formation of a win-stay, lose-shift rule as is the case with rhesus monkeys. Macaques trained on repeated reversals are significantly superior to controls trained on a single discrimination for the same number of trials on subsequent learning set problems (Schrier, in press).

The discrepancy in the results obtained from macaques and chimpanzees and from squirrel monkeys should not occasion surprise. There are strong reasons for assuming that there are important differences in the learning capacities of contemporary Primates and that many of the less advanced forms may differ from macaques and apes in the same way that non-Primate mammals do. Rumbaugh (1971) has demonstrated qualitative differences in reversal learning between talapoins on the one hand, and gibbons and gorillas on the other, which suggest that talapoins learn visual discriminations in a less abstract fashion than apes.

Suppression of transfer from learning set to probability learning problems

In the usual discrimination learning experiment, one stimulus, say white is rewarded on every trial and a second (black) stimulus is never reinforced. In probability learning, both stimuli are rewarded on a set fraction of the trials in proportions like 70:30, 80:20, etc. The optimum strategy for an animal on a probability learning task is to choose the most frequently rewarded alternative on every trial, since such behavior secures the largest number of rewards; this strategy is called maximizing. Animals may, however, distribute their choices to the two alternate stimuli in a proportion which approximates their likelihood of reinforcement; this kind of behavior is known as matching.

Experimentally naïve rhesus monkeys and cats maximize when tested on visual probability problems (Schweikert & Treichler, 1969; Wilson, Oscar & Bitterman, 1964). Experimentally sophisticated rhesus monkeys which had previously been trained on learning set problems also maximize on visual probability problems (Meyer, 1960). But cats with a prior history of learning set training do not maximize on visual probability learning tasks, even when tested for thousands of trials (Poland & Warren, 1968).

These data suggest the likelihood that monkeys differ from cats in their greater ability to suppress transfer from previous learning experiences when such transfer is inappropriate to the task in hand. Use of a win-stay, lose-shift strategy would produce a matching pattern of responding in probability learning and result in fewer reinforcements than a win-or-lose strategy which yields a maximum number of rewards.

4. Conclusions

There is no evidence, not even suggestive evidence, that Primates learn simple problems, or apparently more challenging problems like the double alternation and standard learning set tasks, more rapidly than members of other mammalian orders. These findings do not mean that Primates are dull because they do no better than non-Primate mammals; both Primate and non-Primate mammals can learn such tasks very quickly under favorable conditions. They show instead that mammals generally are rather bright. Although some primatologists have been slow to accept this view, comparative psychologists and ethologists have long recognized that the behavior of mammals is less stereotyped, more individually variable, and more strongly influenced by learning than the behavior of

other vertebrates. "The most striking behavioral characteristic of mammals is their learning ability. Compared with other animals, mammals can learn faster, learn more, remember more and show more insight" (Ewer, 1968, p. 348).

The essentially equivalent performance of Primates and other mammals in learning simple and moderately complex problems indicates that Primates and non-Primate mammals do not differ in many features of learning capacity. Primates and other mammals share a common and rather high level set of mammalian learning skills. But Primates also appear to have something extra. The results of experiments on intertask transfer, e.g. transfer from repeated reversals to learning set problems and extension of the double alternation principle, indicate that at least some Primates have a unique capacity for acquiring abstract general strategies and response rules, more sophisticated cognitive skills than any yet demonstrated in non-Primate mammals.

This review has been restricted to a consideration of learning tasks on which Primates and other mammals have been tested. It would be very misleading to leave the impression that I have provided a comprehensive list of all the probable differences in learning by Primates and non-Primate mammals. Macaques acquire a variety of learning sets, involving more complex relations than the standard task described above, for the solution of multiple sign problems like oddity, matching from sample, and conditional discrimination (Bessemmer & Stollnitz, 1971; French, 1965; Miles, 1965). Chimpanzees show language like behavior (Gardner & Gardner, 1971; Menzel, 1971; Premack, 1971; Rumbaugh *et al.*, 1973), solve intermodal matching problems (Davenport & Rogers, 1970), and learn to recognize their reflections in a mirror (Gallup, 1970). Monkeys and great apes appear to be unique among mammals in respect to the number and variety of tool using performance they emit (van Lawick-Goodall, 1970).

None of these subtle and complex forms of learning has yet been shown in comparable form in non-Primate mammals. But then no one has tried seriously and systematically to develop such behaviors in non-Primates. Since I try not to be a Primate chauvinist, I think the most one can do is to accept tentatively facility in multiple sign learning sets, language-like behavior, etc. as possibly unique primate accomplishments, but watch carefully the results of research with other mammals, especially those, like porpoises, which are reputed to rival Primates in learning ability.

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*The Rockefeller University,
New York, 10021, U.S.A.*

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Consideration is given to different reasons for using animals in research and to problems in making species comparisons. Particular attention is given to studies of processes such as memory which are not directly observed. It is argued that comparisons made in the context of a theory of performance are most fruitful. Finally an experiment is described showing that it was probably premature to conclude that memory is fundamentally different in bird and Man since monkeys display either bird-like or Man-like memory depending on minor changes in the experimental paradigm.

The titles of papers usually convey something of the subject matter but they also tend to reveal a good deal more. Thus if the present paper had been written at the turn of the century, it might have been entitled "The Mental Life of Monkeys" but by the early thirties "Behavior Mechanisms in Monkeys" would have been preferred. In the 1950s a title like "Retention by Monkeys in a Delayed-Matching-to-Sample Task" would have seemed appropriate. However, today I doubt that it would be possible to accomplish a consensus concerning what studies on memory in nonhuman Primates should be called or even whether or not such research is worth doing. The present paper (1) examines the rationale for comparative studies of memory, (2) considers alternative strategies for such research and (3) describes an experiment illustrating one such strategy. First attention will be given to the why and how of animal research on cognitive processes.

1. Why do Research with Animals?

This question would hardly have arisen during the 1930s, 1940s, and 1950s when what we think of now as classical learning theories (Hull, Spence, Tolman, Guthrie, Estes, Skinner) commanded the field. But contemporary graduate students are asking this question, and, judging by their response, they are not satisfied with the answers they hear. Graduate students, as well as their mentors, are becoming less and less inclined to select animals as subjects, especially for research on learning and memory. The only cross-currents in this prevailing trend are (1) an increased focus on ethology or the evolution and ecology of behavior, and (2) a sustained interest in physiological psychology which itself is subject to a growing influence by ethology.

Why this decline of interest in comparative research? Among the reasons commonly given for using animals in research, the two most prominent are convenience and control. Animals can be maintained for extended periods of time to run in experiments more or less at the experimenter's will, without the experimenter being concerned with either the mutual benefit or mutual agreement involved in studies with human subjects. In much the same style the experimenter is able to control important factors such as previous experience and motivational states in his or her animal research. While these are good reasons, they do not begin to answer the question of what the study of animals will tell us about Man. To be sure, it is often added that animal research *is* relevant to human behavior and besides, animal behavior is of interest in its own right. Again, both

arguments may be true, but a perceptive student may discount the latter claim as defensive and want to know in more detail how the studies of animals might be relevant to human functioning. There seem to be at least three answers to this question which define distinct approaches to the study of animals. These will be considered in turn.

Evolution of behavior

Answering how different behaviors have evolved may yield a better understanding of Man's history. How a person behaves in a situation depends not only on the immediate situation itself but may also be a function of the contingencies which his ancestors faced before him. Consider, for example, the problem of aggression and violence in Man. How can the expression of aggression be controlled? Ideally we would like to know how aggression has been expressed and more importantly, regulated, in our evolutionary history. What in our history must be overcome or what can we take advantage of in dealing with aggression? At present we are not even sure whether to view early Man as predator or prey. Other questions having to do with such phenomena as crowding and territoriality make it seem as if efforts to understand Man's heritage will be amply rewarded.

Adaptation

A second, somewhat related, reason for studying animals is to examine how the demands of particular environments, such as an arboreal existence, have been met by changes in anatomical structures and associated patterns of behavior. The distinctive aspect of this approach is that it focuses on adjustments to environments without necessarily worrying about evolutionary history. These adaptations doubtless will be critical to understanding such "flexible" processes as learning and memory in animals and perhaps Man. For example, it appears that the rat has a special ability to associate illness from poisoning with the taste of novel foods even when the poisoning develops long after the food is consumed (for a general review of adaptive learning see Rozin & Kalat, 1971; Seligman, 1970 and Shettleworth, 1972). Human infants may have innate propensities for attending to or perceiving speech sounds compared to nonspeech sounds (e.g. Eimas, Siqueland, Jusczyk & Vigorito, 1971). The study of adaptation holds direct promise and seems essential for the study of the evolution of behavior as well as the study of the laws of behavioral processes, such as learning and memory, to which we now turn.

Behavioral processes

A third reason for using animals in research is to develop principles of the functioning of behavioral systems. If adaptation deals with the what and why of behavior, then behavioral processes are concerned with the how of behavior. By this I intend to encompass most laboratory studies of behavior but would like to concentrate on traditional studies of learning, memory and perception in animals. In this domain, species comparisons may serve to reveal component abilities or processes in a particular task (e.g. a memory task) which could facilitate the development of theories. In some cases it may be valuable to focus on a single species in a line of work, because of some unique traits that the species may manifest. Just as it may be specially convenient to study the axons of squids for anatomical reasons, it may be advantageous to study spatial memory in a

species like the jumping goby, a fish which must be able to remember the location of various tidal pools in order to navigate during low tides. In the same spirit Man clearly has some highly developed and specialized traits such as his language behavior. A substantial question concerns whether memory without language obeys the same principles or works the same way as memory with language. Such work may facilitate the understanding of what is or is not unique to Man. For example, at one time theorists proposed that short term memory was solely auditory and unique to Man, but research with nonhuman Primates (for a recent review see Medin & Davis, 1974) indicates that short-term memory is neither exclusively auditory nor peculiar to Man. The recent research of Rumbaugh, Premack and the Gardners on teaching language to chimpanzees appears to be dramatically broadening our understanding of language and language acquisition. The overall aim of these kinds of direct and indirect species comparisons is to develop theories of information processing without necessarily describing the limits of any one species and without trying to rank order species according to either particular abilities or general traits (such as intelligence).

It seems to me that all three of the reasons just enumerated for studying animals are legitimate and potentially might provide considerable information directly relevant to understanding human behavior. The use of animals in research, especially when considered from a comparative point of view, immediately raises difficult questions concerning how comparisons might be done. The next few paragraphs examine different approaches to this problem. I shall concentrate on processes which must be inferred from performance, such as learning and memory, since they may create special difficulties.

2. How Can One Study Behavioral Processes Comparatively?

The initial focus of laboratory research on learning and memory in various animals was on their similarities. Skinner (1966) reported strikingly similar operant learning in a number of different species of animals and for one brief moment one might have fantasized that one could choose any stimulus, response, reinforcement, and organism and produce the same learning curve! No one ever believed this and rightly so. In one memory task frequently used with monkeys, delayed response, performance varies widely with the incentive, the distinctiveness of cues, the nature of distractions during the delay interval, and practice, just to mention a few factors. It seems nearly impossible to equate all these factors in comparing the performance of two species. Yet, otherwise, the comparison would not be fair.

There are alternative approaches to this problem. In place of attempting to control all factors in making species comparisons, Bitterman (1965) proposed studying functional relationships. The basic idea is that control may be established by systematic variation of factors thought to be important. Bitterman showed that rats stopped responding sooner when reward was removed following consistent reinforcement than after partial reinforcement, while fish displayed the opposite trend. If this pattern of results did not interact with such factors as trial spacing, amount of reward, type of reward, or deprivation, then one might be in a position to conclude that a fundamental species difference in learning was being observed. That is, if performance is changed in the same way by the same variables one might be able to delineate qualitative species differences without precisely equating all factors.

My opinion is that comparative studies of learning and memory would be considerably advanced were Bitterman's approach to be followed, but that studying functional relationships will not prove to be entirely satisfactory. For one reason, it is not clear how to proceed if several factors interact with a species comparison. A more serious concern is methodological and practical. Namely it seems that we shall be required to perform a very large number of experiments to even compare the performance of two species on one particular task. Will we still wonder when we varied some factor such as deprivation whether we varied it enough? The danger is that the study of functional relationships could degenerate into a plodding empiricism where each new factor discovered doubles the number of experiments which must be done.

Success in this enterprise may be more frightening than failure, for success raises the perplexing problem of what a task measures. If monkeys do better than racoons on a memory task such as delayed response what is it that they are doing better? We are interested in the comparative study of memory, not the comparative study of delayed response performance. Tasks become ends unto themselves without some theory of what the tasks measure. The study of mental processes carries with it unique problems because, unlike vocalization or tool using, memory and learning cannot be directly measured. Even if cognitive processes could be measured, it is probably more appropriate to view them as processes rather than as stable fixed quantities or discrete properties. Since processes might be brought to bear in a number of situations producing a variety of performances, it seems more pertinent to ask how memory works in some species rather than asking how much memory animals in that species have. We turn now to an alternative approach to species comparisons which also deals with the assessment of processes.

Another trend in research with animals has been a self-conscious orientation toward the development and testing of theories of animal learning and memory. There are a number of distinct advantages to using theories as a tool in comparative studies of mental processes. First, a theory may lead one to examine detailed aspects of data which might otherwise be ignored. For example, the exact shape of a forgetting curve may suggest whether there are two distinct kinds of memory processes or just one (Medin, 1972). The work of Fletcher and his coworkers shows that particular errors made in delayed response problems are much more informative than the absolute level of performance (Fletcher, Garske, Barron & Gross, 1968). Assessing the predictions of a theory across species may also serve as a guide to both interpreting species differences and developing a theory further. Consider again the difference in the effects of partial reinforcement on extinction of responding in rats and fish. One theory relevant to these data is an attention theory of discrimination learning proposed by Sutherland & Mackintosh (1971). The theory can be modified to handle the species differences and since the theory is designed to account for a range of data, the theory must then make a number of other predictions concerning performance in different learning tasks. In other words the theory retains power because performance on the separate tasks is related by means of the general theory. To the extent that these related predictions are confirmed, a whole range of species differences and similarities may be integrated within the context of a single theory. A final virtue is that a theory can often provide guidance in sorting out which of a possible myriad of variables might be relevant in altering performance in a particular situation. The experiment to be reported here represents an example of this strategy.

3. Spacing Effects in Short-Term Memory

The main interest in the effects of repetitions and the distribution of these repetitions on memory is as a tool in differentiating classes of memory theories. Consideration will be given now to the predictions of some general groups of theories concerning repetition effects.

Probably the simplest theory assumes that memory can be represented by a single memory trace which may vary in strength, this strength being increased by repetitions. During the retention interval, due to either time decay or interference, trace strength decreases at some constant rate toward zero strength. According to this theory, if we hold constant the retention interval between the second presentation of an event and a test, then performance will improve the closer the first presentation is to the second, because less forgetting of the first presentation will have occurred. This is usually described as a "massing" effect.

A variant of this basic theory simply adds the assumption that the trace strength may decrease to some asymptote representing greater than zero strength. The theory could still predict that massed repetitions of an event would produce better performance than spaced repetitions but would allow for the possibility that at least part of the representation of an event might not be subject to forgetting. For example, one might assume that aspects of the event susceptible to forgetting were only represented in a transient "short-term memory" but that aspects might also enter "long-term memory" from which they could not be lost. The form of the retention curve might be used to distinguish this theory from that of the first type. [See Wickelgren (1973) for a more extensive discussion of short and long-term memory.]

There is another set of theories which predicts that spaced repetitions will produce better performance than massed repetitions. In one approach falling under this framework, it is assumed that the number of different cues associated with an event controls retention. Forgetting is produced when fluctuations in the availability of these cues makes it less likely that an appropriate retrieval cue will be available at time of test. Repetitions are helpful because new cues may be associated with the event under consideration. With a constant interval between a second presentation and a test, it is better to have the first presentation at some distance from the second because otherwise the available cue might be so similar that little new learning would occur on the second trial. The advantages of spaced repetitions over massed repetitions would be expected to develop and increase as the retention interval increased. One theory consistent with this description is Estes' stimulus fluctuation model (1955*a,b*). There are a fair number of theories of this type differing considerably from each other on the descriptive level, but having in common the prediction that spaced repetitions are more beneficial than massed repetitions (e.g. see Hintzman, 1974).

How do the data look in relation to these three groups of theories? Studies with human subjects (see Bjork, 1970; Hintzman, 1974 for reviews) point toward theories of the third type, at least for many circumstances. Relevant animal studies are all but totally lacking. Robbins & Bush (1973) reported an advantage for spaced presentations over massed in the discrimination performance of great apes, but they also observed an increase in performance with retention interval (reminiscence rather than forgetting) so this study raises more questions than it answers. The most systematic report on spacing and repetition effects was that of Roberts (1972) using a delayed-matching-to-sample

task with pigeons as subjects. Subjects are presented with a single stimulus, then later on, must select that stimulus from a set of alternate stimuli. A series of four careful studies provided strong evidence favoring the simple trace strength decay model which predicts a massing advantage on the short-term memory (STM) task. Roberts concluded that "the most defensible position, given current knowledge, is that very different mechanisms of STM are at work in Man and bird" (Roberts, 1972, p. 82).

Are there fundamental differences in how memory works in pigeons and Man? There is nothing wrong with hypothesizing species differences to explain the observed performance differences. However, my bias has been to give preferences to explanations based on task differences, partly because of an interest in how widespread certain memory processes might be and partly because task variables can be manipulated, while species differences are fixed (barring behavioral genetics).

Given a bias toward looking for task differences, how does one select which procedural variations to focus on? An analysis of the stimulus fluctuation model suggests that the number of different stimuli used may be an important difference between studies showing an advantage for spaced repetitions and the experiments reported by Roberts. In Roberts' study one of four alternative stimuli was presented on the "sample" trial and, after a delay, a pigeon was given a choice between that stimulus and one of the three other stimuli. Over a series of trials all of the stimuli will be associated with reward and the pigeon must remember which of the stimuli was most recently paired with reward. Preceding trials might exert considerable "proactive interference" on the current trial, since the incorrect alternative on a particular trial might have been correct on the just preceding trial. In other words the subjects must remember which stimulus was *most* recently associated with reward. The human studies cited earlier do not in general have this property since the to-be-remembered items may all differ from each other.

In the experiment to be reported pigtailed monkeys were tested in a delayed-matching-to-sample paradigm. On some days the objects for each trial were different, and on other days only two objects were used. The latter procedure ought to maximize proactive interference while the former procedure might serve to minimize this source of interference. The main interest was in possible differences in the effect of number and spacing of repetitions as a function of whether just two or many stimuli were employed within a day.

4. Method

Subjects

The subjects were six jungle born pigtailed monkeys (*Macaca nemestrina*) 4–5 years old. All animals had received approximately 2 years of training on various object discriminations but were naïve with respect to delayed matching tests.

Apparatus

A Wisconsin General Test Apparatus was used for testing. The three foodwells of the grey foodtray were spaced 15 cm apart center-to-center. The center foodwell was always used for sample presentations while the side foodwells were used for tests. The stimuli were 780 commonly used and manufactured "junk" objects. For a particular day either two different or fifty different objects were used depending upon the experimental condition in effect.

Procedure

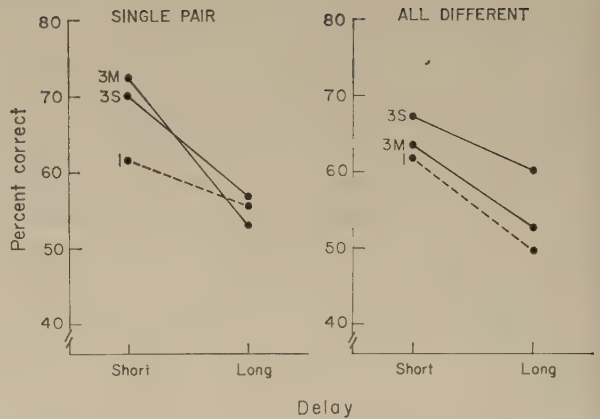
The monkeys were tested five days a week for six weeks on delayed-matching-to-sample problems. The number of different stimuli used varied between days while delay interval, repetitions, and spacing of repetitions varied within each day. On half of the days (randomly selected for each animal) just two objects were used and from trial to trial either could be the sample. On the other half of the days a new pair of objects was used each trial and only one object could be the sample. The sequence on each trial consisted of (1) either one or three presentations of the sample object over the center foodwell, (2) a delay interval of 6, 18, 36 or 72 sec, (3) a two-choice test trial with two objects appearing over the side foodwells and reward always available under the object that had been used as the sample. On a trial when three presentations of the sample were involved these presentations were either massed (6 sec between repetitions) or spaced (36 sec between repetitions). The opaque screen was lowered between successive sample presentations and between sample presentations and the two-choice test. The delay or inter-sample interval was measured from the lowering of the screen after a response to the raising of the screen for the next presentation. The three types of sample presentations and four delay intervals were orthogonally combined to create 12 distinctive conditions. Each of these conditions appeared twice each day, once with the rewarded sample appearing on the left for the test trial and once with it appearing on the right. Since one of the variables to be analyzed is performance on a trial as a function of the preceding trial, a "dummy trial" consisting of a random one of the 24 possible conditions was given on the initial trial. In all, then, 25 trials were given each day. For the 24 trials following the dummy trial the rewarded position was as likely to be different from the preceding trial as it was to be the same as the immediately preceding trial. On days using just two objects each object was equally likely to be correct but a particular object was associated once with each of the 12 main combinations of repetitions and delay intervals. A new pair of objects was used on each of the 15 single pair days. Similarly a new batch of 50 objects was used on each of the 15 all different pair days. Both sample presentations and correct test responses were rewarded with a raisin. Only one response was allowed for the choice tests and the intertrial interval was a constant 12 sec. A day's test session lasted approximately 45 min.

5. Results

The main results are shown in Figure 1, where four retention intervals have been collapsed into short (6 and 18 sec) and long (36 and 72 sec) delays. The left panel displays performance when only a single pair of objects appeared within a day and the right panel shows performance when the objects were different on every trial within a day. These two procedures had distinct effects on performance. On days involving a single pair of stimuli, repetitions facilitated performance at the short delay intervals but at the long intervals percent correct did not differ with repetition conditions and was very nearly at a chance performance level. When the stimuli were unique on each trial, the differences at the short delay interval were small and only spaced repetitions had a large effect on performance. At the longer retention intervals spaced repetitions produced a marked facilitation in matching performance relative to the other presentation conditions.

Statistical tests confirm these trends. At the short delays for the single pair days both massed ($t = 4.30$, d.f. = 5, $P < 0.01$) and spaced ($t = 4.77$, d.f. = 5, $P < 0.01$)

Figure 1. Delayed matching performance as a function of stimulus conditions, delay interval and repetitions. The left panel displays performance on days involving a single pair of stimuli and the right panel shows performance when the stimuli were different on every trial.



repetitions were reliably better than a single presentation but no differences at the long interval approached significance. For the all different pair days no differences were reliable at the short delays but performance on long delays for spaced repetitions was better than either massed repetitions ($t = 2.67$, d.f. = 5, $P < 0.05$) or a single presentation ($t = 4.63$, d.f. = 5, $P < 0.01$).

The single pair condition was associated with considerable proactive interference. One measure of this is the extent to which errors involve responses to either the object or position which was correct on the preceding trial. These results depended upon whether or not the response on the trial preceding an error was correct or incorrect. When the preceding trial response was correct, then 64% of the errors were responses to the object that had been correct on the immediately preceding trial and 61% of the errors were responses to the position that was rewarded on the just preceding trial. These two tendencies were roughly independent. When the response on a trial preceding an error was also an error, there was no significant tendency for errors to be associated with either the object or the position that was paired with reward on the just preceding trial. When the objects are different on every trial, proactive interference can only be defined in terms of responses to previously rewarded positions. There was no tendency at all for this to happen regardless of whether the trial preceding an error was also an error or was correct.

6. Discussion

The configuration of results depended upon whether monkeys were required to remember which object was most recently rewarded (single pair) or just which object was rewarded (all different pairs). Overall, the results on days involving two objects could be handled nicely by a theory assuming a single trace decreasing at some constant rate toward zero since spaced repetitions were no better than massed repetitions, and the repetition advantage did not persist over time. In contrast, when the stimuli were different on each trial, spaced repetitions produced the best performance and this advantage increased with delay interval. This outcome for the trial-unique stimuli can only be handled by theories of the third type discussed, such as the stimulus fluctuation model.

Based on the present study, it appears that results can be produced favoring one set of theories over another set depending upon the particular paradigm chosen. Data from pigtailed monkeys were in accord with those observed in pigeons or in human subjects

depending upon the degree of correspondence of the actual experimental conditions. As of yet, then, we have no conclusive evidence that memory works in fundamentally different ways in pigeons, monkey and Man.

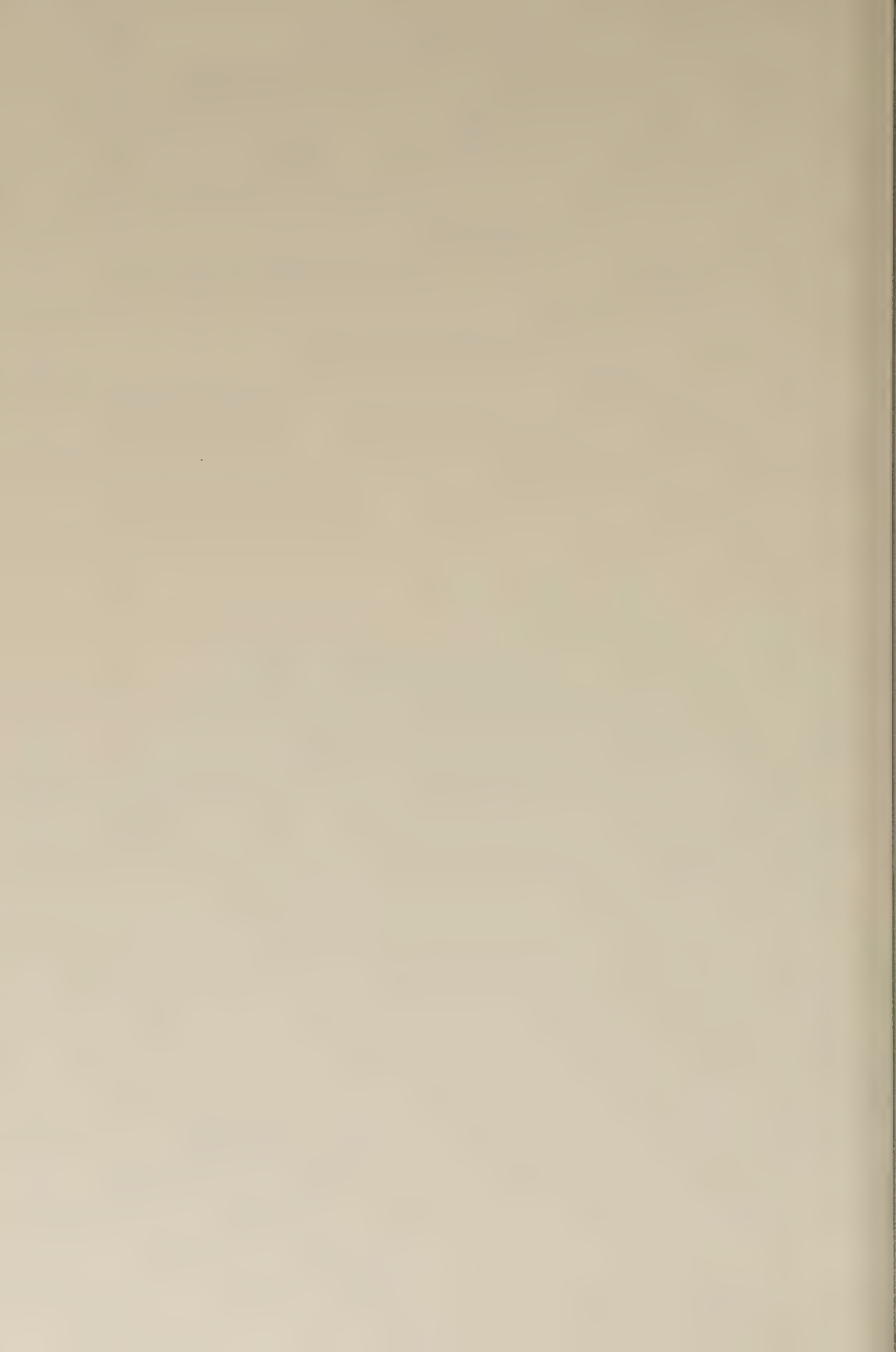
The work described represents only the barest beginnings. Theories are not the abstract entities they are often made out to be. To deal with the present study, theories need to be interpreted or applied more closely to the data. It is completely unsatisfactory to say that one theory fits half the data and another theory fits the other half. It is outside the scope of this paper to do so, but it is possible to extend the stimulus fluctuation model to account for all the present data. This in turn will lead to testable new predictions concerning such things as the pattern of proactive interference as a function of delay interval, predictions which may or may not receive support. We may then find that the modified model gives a much better account of some other sets of human data.

In the comparisons just discussed and in the approach I have been advocating, there is a strong interaction between theory and data. This paper has attempted to illustrate that species and paradigm comparisons become informative in the context of a model or theory to the advantage of both. Further comparative research will answer questions concerning the specificity or generality of particular memorial processes. However, it is clear that we will begin to be able to understand how memory differs across species as we begin to provide an adequate theoretical account of memory functioning in at least one particular species.

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Ernst von Glasersfeld **Signs, Communication, and Language**

Department of Psychology,
University of Georgia, Athens, Ga.,
U.S.A.

and

Yerkes Regional Primate Research
Center, Emory University,
Atlanta, Ga., U.S.A.

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Noting the vagueness and confusion in the literature on animal behavior with regard to the phenomenon of communication, an attempt is made to define "sign" and "communication" from the point of view of cybernetics, drawing also on Susanne Langer's philosophy of symbols. The author argues that neither communication nor language can be successfully investigated as long as the dogmatic behaviorist's taboo against goal-directed or purposive activities is maintained. In accord with recent developments in feedback theory, he shows that the cyberneticist's concept of purpose can be used quite legitimately in the scientific analysis of behavior and that it makes possible a viable classification of signs as well as the discrimination of communication from other types of interaction. In conclusion some of Hockett's "design features" of language are discussed and an attempt is made to formulate criteria for the form of communication that should be called linguistic.

In everyday usage we are not often bothered by doubts as to what is meant by "communication". We take it to mean that one conveys to another what he feels, thinks, knows, or does—and often also what he would like the other to do. Yet, when the life sciences investigate the phenomenon, the everyday concept quickly disintegrates. Colin Cherry, in one of the most valid introductions to communication science, says (1957, p. 6): "Scientific usage frequently needs to be more restricted but should not violate common sense . . ." The study of communication in living organisms has frequently disregarded both the first and the second part of Cherry's admonition.

In these pages I shall try to point out *some* conceptual and definitional adjustments that seem indispensable if we want to clear up the vagueness, ambiguities and contradictions that pervade the literature on animal communication and language. The stress is on *some*. It would take more than a few pages to provide the complete set of unequivocally defined terms needed to map such a wide conceptual area.

In a recent paper, of which I became aware only after having finished this one, Donald MacKay (1972) covers a good deal more ground and comes, I believe, to much the same general conclusions. I shall be content to suggest a number of possible moves towards a less confounding use of "sign" and "symbol", and of the more general terms "communication" and "language". My suggestions are not particularly original. Most of them have been formulated years ago in a branch of science that, in spite of its technicality, is based upon the every-day concept of communication. Cybernetics, as Norbert Wiener (1948) defined it, is the study of "control and *communication* in the animal and the machine" (my italics). Though Wiener has been cited by authors concerned with animal communication (e.g. Altmann, 1967; Hockett, 1960; Sebeok, 1972), most of them limited their interest to two rather specific points while disregarding the general cybernetical framework within which Wiener placed all communicatory processes.

The first of these points concerns the fact that communication events do not conform to the laws of mechanics; i.e. the energy inherent in the communicatory *action* in no way determines the energy involved in the *reaction* (Rosenblueth, Wiener & Bigelow, 1943; Haldane, 1955). For instance, the energy of the sound waves emanating from a man shouting "fire!" is in no fixed or calculable relation to the energy of the event triggered by the shout, an event which may be the explosion that sends a six-inch shell

on its way, the panic of a crowd in a theatre, or some bystander's question "where?". This fact is essential if we want to keep communication apart from mechanical or chemical action-reaction events. If we do not make this distinction, we get definitions of "communication" which include every sort of transaction; e.g. "Communication can be said to occur whenever the activities of one animal influence the activities of another animal" (Alexander, 1960, p. 38).

The second point is the one Wiener made in his introduction to the volume *Cybernetics* (1948, p. 18): "... it is completely impossible to understand social communities, ... without a thorough investigation of their means of communication ..."

Both these points have to do with the *observation* of communicatory events, and that, presumably, is the reason why they were readily adopted by professional observers of animal behavior. Taken out of the cybernetical context, however, they do not elucidate the function a communicatory event might have in the organisation of either a social group or the behavior of the individual. In fact, to adopt *only* these two points is to disregard the very essence of the cybernetical approach.

We do not have to look far to discover the reason why strict behaviorists were reluctant to appropriate anything more from cybernetics. The original essay that laid the foundations of the cybernetical approach had the title "Behavior, Purpose and Teleology" (Rosenbluth, Wiener & Bigelow, 1943). Both purpose and teleology were outlawed in strict behaviorism. As Marler put it (1961, p. 296): "This concept (purposiveness), which may also be associated with an anthropocentric viewpoint, has bedevilled investigations of animal behavior in the past." (And he cites Thorpe, 1956.) A page earlier, Marler states that he finds many of the ideas expressed in Cherry's book (1957) relevant to his investigation and he quotes that author as saying that communication is "the establishment of a social unit from individuals by the use of language or signs". The quotation is taken from the Appendix to Cherry's book (p. 305), but it constitutes only half the definition given there for the term "communication". The other half reads: "The sharing of common sets of rules, for various goal-seeking activities. (There are many *shades of opinion*)" (Cherry's italics). Evidently "goal-seeking" was too close to the devil's activities.

Much the same has happened with references to Shannon's *Mathematical Theory of Communication* (1949). Though it is cited by a number of authors (e.g. Hockett, 1960, 1963; Altmann, 1967; Marler, 1961; Sebeok, 1965, 1972), they do not mention the fact that this theory was conceived, developed and formulated within a very specific context, namely the improvement of communication systems with regard to channel capacity and reliability of signal identification by the receiver, and that, for that reason, it implies the purposiveness of the communicated messages. From this point of view, then, it does not make sense to drop, as Emlen (1960) suggests, all "teleological", "causal", and "contextual" terms from the description and classification of animal sounds. If this were done, the term and the concept "communication" would have to be dropped, too.

Not all investigators of animal behavior, however, are continually preoccupied with exorcising the devil of purposiveness. Menzel, in a recent paper (1973), applies MacKay's definition of communication (MacKay, 1972), which makes the requirement of goal-directedness quite explicit. Earl W. Count (1969), one of the very few who, before adopting the use of cybernetical terms, have gone to the sources from which cybernetics developed, introduces the term "information-ecology" and has no qualms about characterising a living organism as a "purposeful machine".

At this point it should be made clear that, in cybernetics, the words "purpose" and "goal" do not mean exactly what they mean in ordinary English usage. "Teleology has been discredited chiefly because it was defined to imply a cause subsequent in time to a given effect. When this aspect of teleology was dismissed, however, the associated recognition of the importance of purpose was also unfortunately discarded. . . . We have restricted the connotation of teleological behavior by applying this designation only to purposeful reactions which are controlled by the error of the reaction, i.e. by the difference between the state of the behaving object at any time and the final state interpreted as the purpose. Teleological behavior thus becomes synonymous with behavior controlled by negative feedback . . ." (Rosenblueth, Wiener & Bigelow, 1943, p. 24). The function which was called "feedback" is, in Wiener's most general definition (1950, p. 47): "The property of being able to adjust future conduct by past performance."

With regard to the analysis of behavior, the contemporary development of feedback theory (cf. Powers, 1973b) has made it a good deal easier to see the relationship between the purposive behavior model of the cyberneticist and the stimulus-response model of the traditional behaviorist. The S-R theorist has always sought to describe and predict an organism's behavior exclusively on the basis of directly observable stimuli. The feedback theorist, on the other hand, sees the organism's behavior as activity directed towards the minimisation of any discrepancy between a sensory input value (stimulus) and a pre-established "reference value" to which the particular type of sensory input is compared. This discrepancy constitutes "negative feedback"; the larger it is, the more activity the organism has to expend in order to bring the sensory input value to congruence with the reference value. In this sense, and only in this sense, can the organism's activity be called "purposive" and the reference value a "goal".

In her classification of behavioral situations which can be assumed to constitute contexts for communicatory events, Busnel (1969, p. 35) lists seven types (e.g. meeting of the sexes, search for food, territorial defence, etc.). For each of them, feedback theory would posit at least one reference value. The organism's behavior, insofar as it can be reliably recognised as belonging to one of the seven situations, can then be described and predicted in purposive terms as striving towards adequation of the sensory input to the relevant reference value. The more highly evolved the organism, the richer is the variety of sensory feedback it receives and the repertoire of behaviors it employs to adequate it. Francisco Ayala (1974, p. 350) has recently mapped the evolutionary beginnings of information processing: "The most rudimentary ability to gather and process information about the environment can be found in certain single-celled eukaryotes. A *Paramecium* swims following a sinuous path ingesting the bacteria that it encounters as it swims. Whenever it meets unfavourable conditions, like unsuitable acidity or salinity in the water, the *Paramecium* checks its advance, turns and starts in a new direction. Its reaction is purely negative. . . . Greater ability to process information about the environment occurs in the single-celled *Euglena* . . . it not only avoids unsuitable environments but also actively seeks suitable ones. An amoeba represents further progress in the same direction; it reacts to light by moving away from it, and also actively pursues food particles." These capabilities of avoiding, seeking and pursuing can be explained as the result of different simple feedback loops, each with its specific reference value.

The transfer of signals from sense organs to a central processor that computes negative feedback, and from the processor to other organs that implement the adequating activities, is often said to involve communication; but this communication takes place *within* one

organism. When we ordinarily speak of communication, however, we intend what Wiener (1948) called "intercommunication", i.e. the transfer of signals or messages from one organism to another. While the first is explicitly part of a feedback loop, it may not be immediately obvious that the second, too, must be viewed within the framework of a feedback mechanism. Failure to realise this is, I believe, one of the main reasons for confusion in the literature on animal communication.

Considered as an instrument of feedback adequation, intercommunication is a type of activity that appears in the behavioral repertoire of organisms above a certain level of complexity. While all interaction below that level is a matter of "energetics" (Count, 1969), interaction above that level *can* be a matter of "information". We can distinguish the energetic type of interaction from the one involving information by means of the criterion formulated by Wiener (1948) and by Haldane (1955). But this, though a necessary condition, does not yet yield a sufficient definition of "communication". Just as it does not make sense to call all events involving a mechanical transfer of energy between two organisms "interaction", it is misleading to speak of all events involving the passage of information as "intercommunication".

If I land with my face in the gutter, because someone rushing along knocked me down, the transfer of energy may have been very much the same as in the case where a well-aimed punch from a mugger dispatches me into a similar terminal position. Yet, the behavioral situation would be quite different. In the first case the event is "accidental", in the sense that neither I nor my terminal position had anything to do with the rushing person's reference value nor with the negative feedback he was trying to reduce by rushing; whereas in the second case, hitting me and dispatching me into the gutter was indeed "purposive" on the part of the mugger because he had learned in the course of previous experience that these activities were effective in bringing about a coincidence of his sensory input and his reference signal (e.g. my wallet in his hand). We might call the one "fortuitous", the other "instrumental". In ordinary English we should speak of the first event as a "collision" and of the second as an "attack".

The point I am trying to make, however, has to be made, not on the level of words, but on the level of concepts. We can discriminate the two behavioral situations without reference to will, consciousness, mind, or any other concept "associated with an anthropocentric viewpoint"; they can be discriminated by specifying the operative feedback loops—and there is nothing particularly anthropocentric about feedback loops, since they are an integral part, not only of Man, but of primitive living organisms and of machines as well.

To specify an operative feedback loop and its reference value may be a difficult task under certain circumstances. Powers (1973a,b) has suggested an experimental approach to this problem that has the virtue of great flexibility. No doubt, more work will have to be done in that direction. But even if we come across behavioral situations where, in practice, we are unable to specify the organism's reference value with the desired precision, this could hardly invalidate the extrapolation of the theoretical concept, once the "referent" of that concept has been demonstrated and measured in many other cases.

If we apply the discrimination of accidental versus purposive (or fortuitous versus instrumental) activity to the realm of communication between organisms, we find that it is largely compatible with the classification of signs worked out by Susanne Langer (1942). She distinguishes "natural" from "artificial" signs. "A natural sign is a part of a greater event or of a complex condition, and to an experienced observer it signifies

the rest of that situation of which it is a notable feature. It is a *symptom* of a state of affairs." On the other hand, if "arbitrary events are produced which are purposely correlated with important events that are to be their meaning," we have "artificial signs" (Langer, 1948, p. 59).

As examples of natural signs, Langer gives: wet streets as a sign that it has rained (past event); the smell of smoke as a sign of fire (present event); a ring round the moon as a sign that it is going to rain (future event); thunder as a sign that there has been lightning and lightning as a sign that there will be thunder. In every case, the item we choose to consider a "sign" is an event which, in our prior experience, has been reliably correlated with another event; and since, as Hume put it, we believe that future experience will largely resemble past experience, the occurrence of the sign-event leads us to anticipate its correlate. If the perceiving organism has associated a behavioral response with the correlate-event, the behaviorist calls the sign-event a "discriminative stimulus"; if the anticipation, in a cognising organism, leads to an internal representation or thought, the philosopher calls it "inductive inference"; on both levels it constitutes the simplest and most general form of learning and knowledge.

As samples of artificial signs, Langer lists: a whistle means that the train is about to start; a gunshot means that the sun is just setting. The difference between these and the natural signs is clear. Neither the whistle nor the gunshot were (or could be) correlated with the train's starting or the sun's setting *before* they were introduced *qua* signs, simply because they did not happen within those contexts; they were made to happen in order to signify (cf. Hockett's discussion of Paul Revere, 1960, p. 420).

Langer, unfortunately, blurs the issue a little by placing what she calls "fortuitous signs" on the side of the artificial signs. Fortuitous signs are, for instance, the warning cries of animals, such as the various vocalisations of the vervet monkey that alert other members of the group to the proximity of a large or small mammalian or avian predator respectively (Struhsaker, 1967). Similarly, some of the various sounds "produced incidentally to other behaviors" by aquatic organisms (Tavolga, 1960, p. 94) seem to function as natural signs. It would, indeed, be anthropocentric to assume that the vervets invented these cries in order to signal the presence of specific predators; but such an assumption is unnecessary. The distinction Langer presumably had in mind is this: while the signs she calls "natural" are events which, from the human observer's point of view, are in some causal connection to other elements of the event or state of affairs which they signify, the signs she calls "fortuitous" are not. This distinction is the same that creates some difficulty for Hockett in his discussion of the design feature he calls "specialisation" (1960, p. 408). Whether the vervet's utterance of a cry can be causally linked to its flight effort, or whether it is to be considered merely a fortuitous corollary of flight, depends on the sophistication of our causal explanations and does not affect the semiotic status the cry has for vervets. For them it has become a sign—and not an "artificial" one, to be sure—because it happened frequently enough in flight situations to have been associated *by them* with flight and the presence of specific predators. In other words, when a vervet hears such a cry, it responds to it on the basis of its previous experience of the associated situation and, therefore, as though it actually perceived the predator.

To conclude this investigation of the sign-concept, I should like to stress that all the items which, according to our definition, could be called "sign", must have one feature in common: they stand in a one-to-one relationship to the *occurrence* of the event or situation they signify. They are "natural" signs if they co-occur so frequently with an

event or situation that they come to signify it because they become associated with that event *by the receiver*. Alternatively, they are "artificial" signs if, and only if, their association with the signified event or situation has been contrived, in that the sign-event is made to happen by the sender in order to be interpreted as a sign by the receiver.

This differentiation between natural and artificial signs, in many cases, is quite irrelevant to the interpreter of the sign. From the point of view of the traveller lingering at the bar of the railroad station, there is no essential difference between hearing carriage doors being slammed, the station master's shout "All aboard!", or the whistle of the locomotive. All three are signs that the train is about to leave. The traveller does or does not respond to them, regardless of any knowledge as to the fact that the first of them is an integral part of the departure event, while the second and third were contrived and added for purely semiotic reasons. Yet, it is precisely this distinction which enables us to differentiate between events that have the instrumental function of communication and events which have no such instrumental function.

The distinction is parallel to the one suggested for "interaction". It can be made only by reference to the sender of the sign, i.e. by an analysis of the sender's situation, his operative feedback loops, and his activities as instruments for the adequation of his input signals to a specific reference value or goal.

In this context, Tinbergen's concept of "incipient movements" (1952; cited by Altmann, 1967) or incipient behavior in general, may be helpful in explaining the evolutionary development of artificial signs out of natural signs. It would be absurd to consider a bite the sign for a bite; but the biter's opening his mouth may become a sign that a bite is forthcoming. With more experience, an organism could learn that another's raising his head or getting up in a particular way may also herald a bite. Carpenter (1969, p. 46), for instance, describes the development of such an anticipatory sign in the interaction of an infant howler monkey and its mother. Thus the chain of connected events becomes extended and the interval between the sign-event and the signified event becomes greater. The interpreting organism obviously gains an advantage from this extension. But so does the sending organism. If biting was an activity that had become instrumental in keeping the immediate environment clear of other organisms (implying a reference value with regard to which an intruder would constitute a disturbance), the biting organism will soon learn that getting up or opening his mouth is sufficient activity to eliminate his negative feedback. From there to "ritualised" behavior is a small step; and, once certain acts or incipient acts have taken over the instrumental efficacy that originally belonged to the whole chain of which they were merely the beginning, a similar chain may form at the response side of the transaction, replacing the interpreter's immediate response by a subsequent one, and so on until there is no longer any obvious experiential connection (from the observer's point of view) between the sign and the receiver's ensuing activity.

Once we reach such complex levels of semiotic exchange, the sign itself, no matter how we analyse it, gives us no clue as to its signification, nor can we be sure to infer its signification correctly from the receiver's response. In many situations, however, there *is* a fairly reliable clue and it has been intuitively used by every observer of animal communication, though, to my knowledge, it has never been made explicit. It is the simple fact that the sender will cease to emit the sign whenever his environment, which often includes the receiver of the sign, has changed in such a way that the discrepancy between his sensory signals and his reference value has been eliminated. (Note that this approach necessarily

puts relatively permanent incidental changes of the environment, e.g. an animal's tracks or odoriferous deposits, into the class of fortuitous or natural signs.) Marler's compendium of aggregation and dispersal signs (1968) is an example in which the relevant reference values can be easily and accurately specified. These reference values are distances between the individual and other members of his group or between the sender's group and other groups. The heard (received) vocalisations provide feedback as to the actual distance. Whenever there is a discrepancy between that and the reference value, a "distance-increasing" or a "distance-reducing" vocalisation is emitted and the instrumental function, i.e. the purpose, of these vocalisations is the elimination of that discrepancy.

In other situations it may be much more difficult to infer the specific reference value that gives a sign its purposive aspect. It may, indeed, require some form of experimentation, i.e. deliberate, methodical interference of "disturbance" on the part of the observer (Powers, 1973*a,b*). But by varying the sensory input to an organism and by observing both the kind and the amount of activity with which the organism responds to the disturbance, we can eventually establish what the reference value is, to which the organism strives to adequate his input.

This isolation and specification of the reference value or goal is essential if we want to make a distinction between behaviors that have a semiotic function and all the other behaviors that have no such function and are significant only in the sense that they happen to have been experientially associated with certain events or states of affairs. In other words, it is only when we are able to specify the instrumental relation between a sign and the goal towards which *the sender* of the sign is striving, that we would speak of "communication".

Once we adopt the feedback model of behavior, the importance of communication in the development and maintenance of social organisation can be easily explained. What welds a number of individual organisms into a *social* group is not merely the similarity of certain behaviors, but rather the commonality of certain reference values or goals. Because of this commonality, the activity of one individual will frequently eliminate not only his own feedback discrepancy but also the feedback discrepancy of others. This creates a *mutual* or reciprocal instrumentality: others are instrumental in the adequation of my input to my reference, just as I am instrumental in the adequation of their input to their reference. This mutual instrumentality, which has nothing whatever to do with the ethics of altruism, makes for the cohesion of the group.

This is not the place to discuss how concerted efforts, division of tasks, and, eventually, reciprocal dependencies develop out of an original commonality of reference values, but it should be clear that signs, signals, and communication play an indispensable role in the development of any such organisational feats. Sebeok (1972, p. 79) speaks of members of a species becoming "integrated into 'interest communities', joined together, for instance, for mutual protection—like a school of porpoises." Teleki (1973) observed and described the cooperative behavior of chimpanzees in predation and meat-sharing. Malinowski, who half a century ago investigated communication among primitive tribes, said (1923, p. 310): "Speech is the necessary means of communication; it is the one indispensable instrument for creating the ties of the moment without which unified social action is impossible." He used the terms "speech" and "language", and though he discriminated clearly between language functioning "as a link in concerted human activity, as a piece of human action" and language as "a condensed piece of reflection, a record of fact or thought," (*loc. cit.*, p. 312) the two categories have been confounded in almost

everything that has been written about language and linguistic communication since then.

The difference between the use of a signifiatory item as an instrument of action and its use as an instrument of reflection was stressed once more by Susanne Langer. She contrasts "signs" with "symbols" (1948, p. 61): "To conceive a thing or a situation is not the same as to 'react toward it' overtly or to be aware of its presence. In talking *about* things we have conceptions of them, not the things themselves; and *it is the conceptions, not the things, that symbols directly 'mean'*" (Langer's italics).

This is a paraphrase of the basic semantic relation Ogden & Richards (1923) illustrated by their famous triangle. The fact that the symbol is associated with a conception, and only in some cases, and then indirectly, with a "thing", is what releases the symbol from the one-to-one correspondence with the occurrence of an experiential situation. Thus a sign becomes a symbol when it can be used without direct connection to an experiential context. The linguistic items we normally call "words", though they can, of course, be used as signs, are primarily symbols. We can use them in operational loops where neither the input nor the reference values are perceptual and where the activities performed to eliminate discrepancies between the two are not observable behavior but private reflective operations that never become directly manifest in public results. We can use them to modify another's reference values, to supplement his repertoire of instrumental activities, to change his representation of the world he experiences, i.e. his "knowledge".

This removal from the actual experiential situation is not quite the same as the removal Hockett characterised with his design feature of "displacement" (1960, p. 415). The proto-hominoid, who spotted a predator, took fright, and "did not immediately burst out with his danger call, but first sneaked silently away towards the remainder of his band," may, indeed, have achieved a kind of displacement of the danger call that had survival value, but the mere delay does not change the one-to-one correspondence between the sign and the actual perceptual situation. The danger call remained wholly instrumental in a feedback loop that was disturbed by the sensory input provided by the actual predator. The danger call will become a symbol only when a later hominoid can utter it *without* having spotted a predator and when the other members of the band can hear it *without* taking flight. The displacement characterised by Hockett may well be a plausible step in that development, but it is at best a preparatory step and, as such, not a criterion for the symbolicity that is an essential feature of "language".

Hockett subsequently (1963, p. 10) introduced an additional design feature that implies symbolicity, i.e. "prevarication", and he remarks: "It ought to be noted that without the property here labelled 'prevarication', the formulation of hypotheses is impossible." It seems unlikely that we could ever establish *by direct observation* that another organism's sign is uttered in the hypothetical mode, unless the organism already has a conventional sign for indicating this. What primatologists have called a "play-face", i.e. a sign indicating that a subsequent aggressive behavior is not to be taken seriously, is a case in point. It should also be noted that in Piaget's theory of cognitive development the symbolic function first arises in play (Piaget, 1967, p. 90).

Though the meaning of symbols is conceptual and, therefore, by definition inside an organism and not directly observable, their function can be demonstrated. Premack in his artificial communication system with the chimpanzee Sarah, introduced questions and negation at an early stage (Premack, 1971). Both require conceptual representations

that come very close to what we call an hypothesis and the successful handling of a combination of the two proves the presence of some symbolicity.

Successful handling, in this context, is not a question of behavior, if by "behavior" we intend the responses which the behaviorist dogma has sanctioned as observable. That an organism handles a symbol successfully can be shown only by the use of other symbols, because the reference values as well as the "inputs" that have to be adequated to them are not on the perceptual level. If, for instance, we show an orange to a chimpanzee and then ask him, by means of any signs he has learned to use, "Is 'apple' the name of this?", the correct response is to say "No". What makes it correct is not the perceptual difference between the apple-sign and the orange (any sign would be different from an orange), but the difference between the concept associated with the apple-sign and the concept by means of which the orange is recognised as an orange. The kind of item we mean by "concept of an orange" has been discussed with admirable lucidity by Bronowski & Bellugi (1970). In order to respond correctly, a comparison has to be carried out on the conceptual level, which is not the case in the usual discrimination tasks given to experimental animals. In this very specific sense the combination of question and negation is a test for symbol manipulation.

When we ordinarily use the word "language", we certainly take it for granted that we are dealing with a system whose elements are capable, not only of displacement, but also of functioning as symbols. But there is also a more easily discernible feature which we take for granted. What we call "language" must be a combinatorial system of symbols which, to quote Hockett (1960, p. 418) once more, "... provides certain patterns by which these elementary significant units can be combined into larger sequences, and conventions governing what sorts of meanings emerge from the arrangements." Hockett judiciously avoids the term "syntax" and speaks of the "sorts of meanings that emerge from the arrangements". This is important because linguists have traditionally understated, if not disregarded, the semantic dimension of syntax. The crucial feature, then is not that language has rules for stringing symbols together, but that the stringing together adds another level of meaning. "To paint a red house" contains the very same elementary word-symbols as "to paint a house red", but some of the relational concepts indicated by the two strings are different. It is this feature of combinatorial meaning that leads to the "openness" of linguistic communication systems and gives the user the possibility of "productivity" or "novelty" of expression. Combinatorial meaning and symbolicity of the elements, thus, yield a reliable criterion for distinguishing between language and other communication systems whose elements have a necessary one-to-one correspondence to the occurrence of events or states of affairs in the experiential context in which they are used.

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Roger S. Fouts

*Institute for Primate Studies,
Department of Psychology,
University of Oklahoma, U.S.A.*

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Language: Origins, Definitions and Chimpanzees

Language and its evolutionary origins are examined in the light of empirical data from studies on artificial language acquisition, human language acquisition in the chimpanzee and the definitional problems surrounding language. Rather than providing solutions, questions are raised in regard to the various approaches to the problems of language origin and definitions of language.

Speculation concerning the evolution of Man's behavior has a history of producing controversy in the scientific world. Futile debates have raged in attempts at a resolution, but then failed because "armchair speculation" was more the rule than the exception. Behavior of early Man, for the most part, has not been subject to anything approaching empirical validation. For language this has been especially true. Scholars have dealt with the problem of language origin for nearly 200 years (Hewes, 1973*a*). Theories on language origin were only limited by an individual scholar's imagination. The sky was the limit, and as Hewes (1973*b*) points out, in 1866 the 'Société de Linguistique de Paris' banned any papers dealing with the subject for just that reason; since most were mediocre or crackpot in nature.

One might view these early attempts at explaining language origin as being premature, to say the least, based on the available evidence. Nearly 100 years later the question is beginning to be dealt with again by anthropologists (e.g. Hewes, 1973*a,b*, and Hill, 1972), but this time with some empirical support. Interestingly, the empirical evidence is coming predominantly from psychologists (Gardner & Gardner, 1969, 1971; Premack, 1971; Rumbaugh, 1973; and Fouts, 1972, 1973, in press). But the blending of the two disciplines can hopefully produce viable progeny for understanding of human behavior.

The use of chimpanzees for these studies is a logical choice since the chimpanzee is one of Man's closest evolutionary relatives. The evidence in this regard has been documented in such research areas as blood protein, chromosomal characteristics and the remarkable similarity of the chimpanzee's brain to Man's. But the similarities go beyond physiological characteristics to behavioral similarities found by scientists studying chimpanzee behavior in his natural habitat (e.g. Goodall, 1968). The area of naturalistic observation does not seem to be running out of new surprises for those individuals who have relied on the absence of empirical data in order to make statements about what a chimpanzee cannot do and humans can.

Presently there are two different theories concerning language origin in Man. Gordon Hewes (1971, 1973*a,b*) proposes that language was gestural in its origin and he uses the empirical evidence from studies on chimpanzee language acquisition and studies on sign language in humans to support his contention. On the other hand, Jane Hill (1972), as an example, disagrees with the gestural origin of language and supports a vocal origin. She states that a "chimpanzee who spent a lot of time doing deaf sign . . . would soon be

training their chimpanzee Lana, is capable of reading and writing in a computer (PDP-8) controlled language training program. Using geometric lexigrams (white) displayed on various colored background keys they were able to study Lana's production of sentences and also sentence completion.

This experiment has managed to completely remove the human element and therefore strictly control for cueing while having a complete record of Lana's responses in terms of pressing the keys.

Lana was presented with sentences, valid or invalid beginning, in the first two experiments. She had to complete the valid sentences in order to be correct and press the "period" key on the invalid sentences which would remove them from the display. In the second two experiments Lana was presented with only valid sentences but each experiment had different options for her use. In these four experiments Lana demonstrated, in her significantly above chance level of responding, that she was capable of discriminating between valid order in the beginning of sentences and invalid beginnings. These well controlled experiments showed that word order was important to Lana's sentence production. As a result this can be interpreted as an ability to respond to something similar to (if not the same as) syntax in human language. If word (lexigram) order was something that Lana could not respond to, then she would have completed sentences regardless of their valid or invalid beginnings.

2. American Sign Language Studies

Gardner & Gardner (1969, 1971) initiated the first successful study of a chimpanzee acquiring a human language in 1966. Their subject was a 10-14 month old chimpanzee named Washoe. Washoe was reared in an enriched environment (as compared to the environments typically provided for captive chimpanzees) which provided her with a human companion during all of her waking hours. American Sign Language for the Deaf (Ameslan) was used exclusively to communicate with her and while in her presence.

Washoe acquired individual signs by imitating the human signs around her in the same fashion as human children do. She was also taught signs by mechanically molding her hands into the correct form of the sign while in the presence of the exemplar representing the sign. The molding method of training was a more efficient method in terms of increasing her vocabulary (Fouts, 1972). But simple labeling or vocabulary size is not the most salient feature of language in a human or a chimpanzee. The combining of signs by Washoe is more interesting relative to sheer vocabulary size and she began to produce sequential combinations by the time she had a vocabulary of eight to ten signs. This has also been noted in other chimpanzees when they have begun to acquire a vocabulary of signs (Fouts, 1973). Washoe's combinations were used in contextually correct situations (e.g. *key open please blanket* to have locked blanket cupboard opened) and she evidenced a preference for sign order which can be interpreted as demonstrating a syntactical capacity on her part. Certainly the evidence from Premack (1971) and Rumbaugh *et al.* lends credence to this interpretation.

Washoe's vocabulary and her usage of it were systematically recorded by the researcher. In addition, she was tested in her vocabulary in a double-blind vocabulary test that controlled for the possibility of cueing. Her performance on this was 53 correct out of 99, far above the chance expectancy of three correct. Her errors on this test fit into

conceptually related categories; for example if the exemplar was an animal, her errors were most likely other animal signs.

The sign language studies on chimpanzees has been expanded to several chimpanzees at the Institute for Primate Studies at the University of Oklahoma. An early study here using four chimpanzees found that there are "individual differences between the chimpanzees in their ability to acquire the signs and that some signs are consistently easy or difficult for the chimpanzees to acquire (Fouts, 1973).

Research is in progress concerning chimpanzee-to-chimpanzee communication using Ameslan (Fouts, Mellgren & Lemmon, 1973) at the Institute. The goal of this study is to introduce Washoe (who is now at the Institute for Primate Studies) into a signing dyad of Booe and Bruno (two five-year-old males with vocabularies of more than 40 signs). We hope to observe sign acquisition by Booe and Bruno from Washoe, since she has a larger vocabulary (over 160 signs) and is more experienced signer. Washoe has been observed in the past to sign to other chimpanzees quite readily. Presently Booe and Bruno are signing to each other in such situations as play, food sharing and mutual comforting. We are merely waiting until their intraspecific communication reaches a preset reliability criteria before Washoe is included.

Another completed study examined the conceptual ability of a seven year old female chimpanzee named Lucy (Mellgren, Fouts & Lemmon, 1973). This study also examined the effect of a new sign on the conceptual category. Lucy was presented with 24 different fruits and vegetables. Over a period of four days she was asked what the fruit and vegetable items were. She had five food related signs in her over 70 sign vocabulary (*food*, *fruit*, *drink*, *candy* and *banana*) to respond to them. After the fourth day she was taught the *berry* sign to a cherry. This sign remained very specific to cherries and did not generalize to other berry-like items. This may have been because of her linguistic development of that time; since it is comparable to children who early in their linguistic development use words in their vocabulary in a very generic sense (all four-footed furry animals are dogs) and later they became more specific. Language seems to be a process of inhibition since it appears to move from the general to the specific. Just as interesting was Lucy's conceptualization of the fruits and vegetables. For example the four citrus fruits were predominantly labeled by Lucy as *smell fruits*. She called a radish a *food* for three days and then after taking a bite out of it she labeled it a *cry hurt food* and continued to use *cry* or *hurt* or both to describe it over the final eight days of data collection. A watermelon was labeled as a *drink fruit* and a *candy drink*, but was predominantly described with the *drink* sign. She showed a clear preference to label the fruit items with the *fruit* sign and the vegetables with the *food* sign.

The ability to recombine signs in their vocabulary to describe novel items or situations is very typical of the chimpanzees using signs. For example, Washoe refers to ducks as *water birds*, and once when she apparently did not know a sign for some brazil nuts, since she asked for them by signing *rock berry*.

Several of the chimpanzees who are being reared in human homes near the Institute appear to have large English understanding vocabularies. Fouts, Chown & Goodin (1973) have examined the relationship between the English understanding vocabulary and the Ameslan production vocabulary in Ally, a three-year-old male. Initially Ally was tested on his understanding of ten spoken English words by being given vocal English commands. After Ally had met the criterion for understanding these vocal English words, they were divided into two lists of five words each. An experimenter then would teach

a sign using only the vocal English word as the exemplar then a second experimenter would test Ally on the objects to determine if the sign would transfer to the visual object. Ally successfully transferred the signs he learned for the vocal English word to their physical referents. In this manner he demonstrated a behavior similar to second language acquisition in humans, but note that it is across modalities (auditory-visual) rather than being within modalities (auditory-auditory), which is more typical.

Another study examining productivity in terms of understanding novel combinations of signs was just completed using Ally. This involved teaching Ally to obey a command that had him choose one of five objects and put it one of three places. Once Ally learned to do this he was tested on novel commands and he performed above chance in testing. Testing was done in a situation that controlled for the possibility of cueing by being a blind-testing situation.

3. Definitional Problems in Language

As can be seen from the previous section chimpanzees have demonstrated a competence in language skills similar in degree to those displayed by humans. These findings have generally been considered in relation to various definitions of language. Most of these definitions have attempted to exclude the chimpanzee from the realm of language.

An often quoted paper in this regard is one by Bronowski & Bellugi (1970). In this article they list five characterizations of language. (1) Delay between stimulus and utterance, (2) separation of affect from content, (3) prolongation of reference, (4) internalization and (5) reconstitution. They feel that Washoe has met the first four, but fails to demonstrate reconstitution. They define reconstitution by stating "the structure activity of reconstitution, which consists of two linked procedures—namely, a procedure of analysis, by which messages are not treated as inviolate wholes but are broken down into smaller parts, and a procedure of synthesis by which the parts are rearranged to form other messages" (p. 670). They conclude the following: "What the example of Washoe shows in a profound way is that it is the process of total reconstitution which is the evolutionary hallmark of the human mind, and for which so far we have no evidence in the mind of the non-human Primate, even when he is given the vocabulary ready made" (p. 673). It is interesting to note that they admit using "no evidence" as the main support of their contention. Using "no evidence" is a well established procedure for coming to premature and incorrect conclusions. Most certainly the evidence presented in the previous section demonstrates that chimpanzees have the capacity for reconstitution (e.g. Lucy's reference to a radish as a *cry hurt food*, Washoe's reference to ducks as *water birds*, and so on). And if Bronowski & Bellugi's contention that reconstitution is the "evolutionary hallmark of the human mind" is correct, then we must assume that the capacity for language was in the repertoire of the species before the Great Apes evolutionarily split off from hominid evolution. Another alternative is that the basis of language is not unique to language *per se*, but may actually be the basis for other behaviors and language is just one product.

Hebb, Lambert & Tucker (1973) state that "True language is distinctive in its combination of two or more symbolic acts (words or gestures) into one situation and in the ready recombination of the same parts in another situation or for another purpose" (p. 56). This is in essence the same criterion that Bronowski & Bellugi (1970) refer to as reconstitution. But Hebb, Lambert & Tucker come to an entirely different conclusion by stating that: "By the criteria proposed, Washoe has language: she combines symbolic

gestures (from American sign language) in various ways with the intent to communicate" (p. 56). Therefore, we have two opposite conclusions in regard to a chimpanzees capacity for language using the same criteria. If Bronowski & Bellugi (1970) and Hebb, Lambert & Tucker (1973) are correct in their criteria for language then chimpanzees obviously have it.

Likewise one could conclude from Schneirla (1972) that chimpanzees have met the criteria for the essential characteristics of communication in human society which he lists as: "(1) its symbolic and conventionalized character, (2) its directive function (i.e. using symbols to influence others), (3) its intentional use in social situations, and (4) its capacity for arrangement or rearrangement according to the requirements of meaning (cf. Bierens de Haan, 9)" (p. 420). It is again interesting to note that the fourth criteria is remarkably similar to Bronowski & Bellugi's (1970) reconstitution and the major criteria of Hebb, Lambert & Tucker (1973).

It appears that there is the potential for as many definitions of language as there are scientists who have some interest in this area.

At this point I prefer to leave the definition of language up to the individual reader. Rather than risking the possibility of making the opposite error of those who have emphasized the differences by emphasizing similarities which may not be important for the basis of language.

One final comment is in order regarding the criticism that Washoe's acquisition of signs was the result of intensive training efforts and is therefore quite different from human language acquisition. Again, this kind of criticism is based on misconception concerning the Gardners' (1971) project. Granted, Washoe was in the constant care of humans, but the vast majority of this time was not spent on intensive language training, but rather in exposing her to human contact and human communication. Only a minimal amount of time was spent in intentional training. Washoe acquired the signs quite readily and I have found in my research that only 3 or 4 hr a week of training are necessary for a chimpanzee to acquire a viable vocabulary. The main training component appears to be the teaching and exposure of chimpanzees to a sign language vocabulary. Once they have this they begin to combine these signs in a spontaneous manner. Sign language training in a chimpanzee is quite easy to accomplish if the chimpanzee is used to human contact, and welcomes such contact.

4. Comments on Language Origin

The speculation concerning language origin has the problem of not having any empirical fossil records or behavioral evidence for language in early Man. Presently comparative studies on chimpanzee's language acquisition is available for this. But, as has been shown, this offers little support because there is no generally accepted definition or criteria for language. Also, the controversy of whether or not early Man's language was gestural or vocal is not a question that seems to have an easy answer. For one thing, the mode is not a major criteria for language. However, if one thinks that chimpanzees have met a definitional criteria for language then it could be assumed that the basis of language may have been present in our ancestors before the pongid and homid line of evolution became separate. But, one further question must be answered before this conclusion is viable; it must be determined whether or not the capacities for language in humans and chimpanzees were the result of parallel evolutionary development in the two extant

species (man & chimpanzee) or whether they originated from a common ~~the~~ neurological basis.

species (Man and chimpanzee) or whether they originated from a common neurological basis.

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Timothy V. Gill
Duane M. Rumbaugh **Mastery of Naming Skills
by a Chimpanzee**

*Department of Psychology,
Georgia State University,
Atlanta, Ga. 30303,
U.S.A.*

and

*Yerkes Primate Center,
Emory University, U.S.A.*

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The acquisition of naming skills by a chimpanzee in a computer-controlled language-training situation is described. Initial training consisted of presenting one of two exemplars coupled with the question, *What name of this?* Upon mastery of that phase, two transfer-of-naming tasks were given, results of which demonstrated that the subject had come to learn that things can be referred to by name.

Several attempts have been made in the past at establishing verbal linguistic behavior in nonhuman Primates. Efforts to develop spoken languages (e.g. English or Russian) with chimpanzee subjects have met with little success (cf. Kellogg, 1968; Ploog & Melnechuk, 1971). The research paradigm involved in these studies followed basically the same pattern: placing a relatively young chimpanzee (initially less than eight months old) in a natural human home environment, and treating it much like one would treat a human child. In several of these studies, a human child was included with which to compare the development of the chimpanzee. The study of Donald and Gue (Kellogg, 1968) is one of the most publicized works in this area. In this comparative study of child and chimpanzee, every attempt possible was made to stimulate the chimpanzee into verbalizing. This was to no avail, however, for although Gue appeared to understand the simple words and commands of the Kelloggs, she could/did not speak.

The study by the Hayes's (Hayes & Hayes, 1951, 1952*a, b*; Hayes & Nissen, 1971) employed a fairly strict procedure in their attempts to teach the chimpanzee Viki spoken English. They attempted to teach Viki language by manually shaping her mouth into the proper form for emitting human speech patterns. After 6.5 years of training, Viki was capable of mouthing the *unvoiced* whispers of the words "mama," "papa," "cup," and "up." This limited success can hardly be taken as a breakthrough in inter-species communication, but it did seem to prove that even over a long period of time and under fairly strict conditions, spoken natural language could not be established in the chimpanzee, Viki. The chimpanzee involved appeared to be very bright otherwise, mastering a variety of complex tasks with minimal difficulty (Hayes & Nissen, 1971).

Recent research conducted by Lieberman (1968; Lieberman, Klatt & Wilson, 1969; Lieberman, Crelin & Klatt, 1972) has demonstrated that it is physiologically impossible for various nonhuman Primate forms (among them the chimpanzee) to emit the majority of sounds that constitute phonemes in natural human language. The question remains, however, as to whether chimpanzees are capable of another form of language, for spoken language is not the only medium of communication that humans utilize. If the similarities between the vocal tracts of various human and nonhuman Primate forms (Lieberman, Crelin & Klatt, 1972) indicates a common ancestor, then perhaps the chimpanzee is capable of a language form similar to that postulated for Neanderthal Man, that is, one

comprised of gestural as well as vocal signals (Hewes, 1971, 1973). Current research in language development in chimpanzees has utilized gesture and manipulation in place of vocal signs and has met with a moderate degree of success.

The Gardners' (1969, 1971; Fouts, 1972) project with the chimpanzee Washoe has stimulated a series of experiments in this field. In their pioneering project they employed the American Sign Language (ASL), a gestural system of communication utilized by the deaf in the United States and Canada. They devised a laboratory setting emphasizing a minimum amount of confinement and a maximum degree of social interaction with human companions who communicated almost exclusively in ASL.

Their choice of ASL as a means of communication seems to have been a good one, for Washoe mastered a large number of signs and used them appropriately in many situations. At the end of the first 30 months of the project, Washoe had mastered 85 different signs, many of which were objects' names. Washoe also used signs in various combinations, usually involving only two signs but sometimes more (Gardner & Gardner, 1971).

A second study utilizing a unique approach to the problem of language development in a normally non-linguistic organism was conducted by Premack (1970, 1971; Premack & Premack, 1972). This study approached the problem from a different viewpoint than the Gardners'. Whereas the Gardners relied heavily upon modeling and imitation in teaching vocabulary to their chimpanzee, Premack was more interested in devising learning situations for teaching language principles to a non-linguistic organism. Premack chose pieces of plastic that varied in size, shape, color, and texture as the mode for communication with his chimpanzee subject, Sarah.

Premack claims to have succeeded in teaching Sarah a number of basic concepts relevant to language through a series of well defined steps. Among these were the interrogative, sameness/difference, the use of Yes and No, the concept "name of," and dimensional classes such as color, shape, and size. The results of Premack's tests would be more convincing if he availed to the reader a more complete record of procedures and data. The bases for his conclusions are frequently obscure and not supported by specific data. Too, unlike the procedure used by the Gardners, Premack's procedures severely limited the ability of Sarah to respond in a creative manner, particularly during testing sessions.

The concept of "naming" things in the environment is a process basic to language. Lancaster (1968) states that the ability to name objects allows Man to refer to the environment surrounding him and to express himself in a manner that is not just concerned with his own motivational state. Concerning the evolution of environmental reference (object naming), Lancaster concludes that Man's ability to use tools is also unique and that perhaps the use of tools and environmental reference are closely related. The research by Goodall (1967), who discovered the use of tools by chimpanzees in the wild, and the language research by the Gardners and Premack seemingly refute this thesis that man alone is capable of tool-use and environmental reference. It does not refute, however, the premise that tool-use and object-naming go hand in hand in the evolution of Man. Accepting the great apes as Man's closest living relatives, then the use of simple tools and the ability to learn rudimentary language principles by chimpanzees seems logical.

There is a difference, of course, between actually assigning symbols as names to objects and learning objects' names assigned previously by another agent. The former involves creating a symbol or label of some type for an unnamed object, while the latter involves

learning a pre-established name for an object. Washoe and Sarah have mastered the latter; however, to exclude the possibility of their being capable of giving names to objects is unwarranted, for Washoe has invented signs on her own several times (Gardner & Gardner, 1971, pp. 138-139). Too, Washoe has given clear evidence of "understanding" that objects' names are not the objects *per se*, for she frequently both asked for objects' names and even modified the names appropriately from time to time.

Research dealing with the ability of humans to name objects or with the developmental aspects of learning the concept "name of" is virtually non-existent. This is likely due to the fact that this is the first concept that occurs in language: people and objects are first named by the parents and subsequently they are learned by the child as he develops physiologically the ability to speak. Roger Brown (1958), in an article dealing with the establishment in children of the concept of naming things, followed the above thesis and further states that things are first named so as to categorize them in a way that is most useful for the child. For example, a car is first called a car rather than a specific make of car, while a spoon is called a spoon rather than the general term silverware. In some cases, naming moves from the concrete to the abstract (spoon to silverware), in others from the abstract to the concrete (car to type of car).

Even though the ability to name things in our environment is basic to language, in language research it has been essentially ignored. The studies of Premack and the Gardners have demonstrated that naming skills and related conceptual processes can be studied in the chimpanzee. Their findings have prompted further research in this area, including the study reported in this paper.

Currently underway at the Yerkes Primate Center is a language development study that also utilizes a chimpanzee as the subject. A team of scientists* from Georgia State University, the University of Georgia and the Yerkes Primate Center has devised a computer controlled language training system for investigating the language skills of young apes. The subject involved at present is a young chimpanzee, Lana, who has been in the training situation for about seven months prior to the conduction of the studies that constitute this paper.

The computer system, related hardware and language devised for this project have been described elsewhere in detail (Rumbaugh *et al.*, 1973) and only the main features will be described here. Basically there are three main features to the entire system—the computer, the language, and the hardware involved in Lana's testing chamber. A PDP8-E computer (Digital Equipment Corp., Maynard, Mass.) is utilized as the intermediary between Lana and the outside world, functioning simultaneously as a language analyzer, an agent that dispenses requested items and as recorder of all language interactions that occur. It also allows for training to continue 24 hr a day, seven days a week, a most important aspect, it would seem, if one should hope to establish language in a normally non-linguistic species.

The language involved, called Yerkish, is derived from the correlational grammar developed for computer applications in the area of automatic language analysis and machine translation (von Glasersfeld, 1964, 1970). The words of Yerkish, termed lexigrams, are each assigned to a class and have been restricted to one and only one meaning

* The authors are a behavioral specialist and principal investigator, respectively. Other team members are Ernst von Glasersfeld, psycholinguist, and Pier Pisani, computer specialist, both of the University of Georgia; Harold Warner, biomedical engineer, and Charles Bell, electronics technician both of the Yerkes Primate Center. Also, Josephine V. Brown of Georgia State University serves as a consultant.

of a corresponding English word to avoid as many ambiguities as possible. There are a number of different lexigrams in most classes and the members of each class are treated as equivalents by the language system. All classes are restricted on a conceptual level as to the other classes with which they may be correctly correlated. The grammar involved is of the general form subject-verb-object, with sentence markers corresponding to intonations in spoken English coming at the beginning of the sentence. Since the inception of training, Lana has been required to attend to both the meaning of specific lexigrams and to their appropriate place in a sentence. She quickly became adept at sentences such as *Please machine give M&M period*, which is the general syntactical form of food and object requests. As all word usage that transpires is recorded, novel combinations can be studied in detail to determine if Lana is developing a consistent syntax on her own.

Lana's keyboards (two at present, each one foot square) each contain 25 rectangular acrylic keys, on the surfaces of which are embossed specific lexigrams. Each lexigram is composed from one or more of nine distinct stimulus elements and has a particular color background pertaining to the class to which the word belongs. Outside of Lana's chamber is a functionally equivalent keyboard, utilized by the experimenter in attempts at conversation with Lana. As each operative key is depressed, it becomes fully illuminated, while at the same time the elements of the particular lexigram are projected on one of a series of rear-projections screens located both above Lana's keyboard and outside of her room above the experimenter's keyboard. Thus Lana is afforded immediate visual feedback as to the key she has just depressed. There are two sets of projectors in each area, one to send messages and the other to receive them.

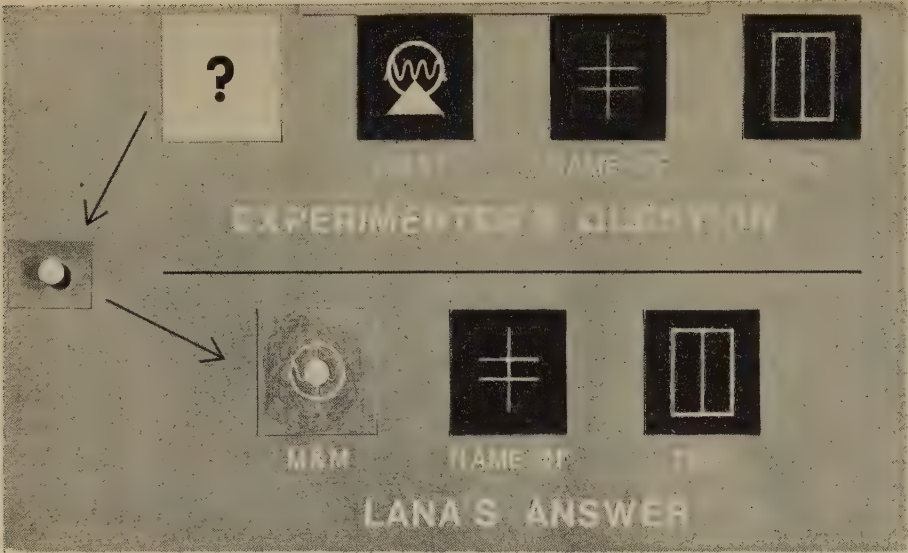
That Lana has come to attend to and read these projected images was the subject of a recent study by Rumbaugh, Gill & von Glasersfeld (1973). In this study, various correct and incorrect sentence beginnings were presented to Lana through her projectors. Her task was to selectively complete the sentence (in the case of a correct beginning) or to erase it through depression of the *period* key (in the case of an incorrect beginning). For example, a correct beginning would be *Please machine give*, to which Lana could selectively respond with *juice* or *M&M* and obtain that reward, whereas an incorrect beginning would be *Please give machine*, to which the proper response would be depression of the *period* key. It was concluded that she could indeed read the projected images, paying attention both to the order of the lexigrams and their meanings.

Throughout the course of Lana's training, she has come to use a number of lexigrams that correspond to certain items in her environment. She has had ample opportunity to use these lexigrams, but only in a manner that resulted in receiving the item. For example, she daily asked *Please machine give piece of chow period* and received a piece of monkey chow each time for so doing. It was therefore of interest to determine, if possible, the answer to the following question: Could Lana "name" these objects by correctly using the lexigrams established for them in a different situation? More specifically, if asked the question "What is the name of this?" could she respond correctly? If language acquisition can be seen as a number of steps, with the first and most fundamental being the ability for environmental reference, then these indeed are important questions to answer.

Also included in the process of language acquisition is the ability to respond selectively to the intonations used in a particular sentence. Two sentences composed of the same words can have entirely different meanings depending on the intonations used by the speaker. Similarly, it was necessary for Lana to come to respond differentially to sentences



Plate 1. An example of a question posed through use of the experimenter's keyboard to Lana in the training program for acquisition of naming skills. With "M&M" as the exemplar, the correct answer expected of Lana is also given.



presented to her in a visual manner by paying particular attention to the sentence markers. In the present experiment, she had to learn to pay attention to the particular marker indicating the interrogative. She also had to learn to respond in a declarative manner, for at the time of these experiments all of her training had been in the use of the "request" type of sentence.

If Lana could answer the question "What is the name of This?" then at least one of the basic components of language could be said to have been established. If not, then perhaps all that was being obtained was an elaborate series of operant tasks. The following study served to answer this question. It was predicted that she could, and indeed would, correctly name familiar objects in her environment.

1. Method

Subject

The subject of this experiment was a female chimpanzee (*Pan*), Lana, who was 2.75 years old at the time of testing. Lana had been involved in the language training situation for seven months prior to the present study. She had become totally dependent on her language capabilities for all of her nourishment and any stimulation that she might have desired (e.g. movies to view, music to listen to, and her seemingly insatiable desire to be tickled).

Apparatus

The apparatus involved in this study has been described in the introduction to the paper.

Procedure

Due to the dynamic nature of the language training situation, any *specific* step-wise procedure was impossible to establish. As one of the major strong points of the system is its flexibility, it was decided to set up, in outline form, what was to be accomplished and the manner in which it hopefully could be established. The specific aim, of course, was to see if Lana could correctly name familiar objects in her environment, objects for which the lexigrams had frequently been used. The general procedure was as follows:

(1) *Pre-Training*. This phase involved establishing the specific key depression response "*item-name*" *name-of this period* to the query ? *What name-of this*, where "*item-name*" refers to the lexigram previously established as the symbol for the exemplar in question (Plate 1). The *of* portion of *name-of* is included with it as a single lexigram rather than using the separate lexigram for *of* due to the previous establishment of the use of the word "*of*" in connection with *piece of*. The use of *of* in *piece of* indicates something different than the *of* that is used in *name-of* and thus to avoid ambiguities it became part of the word *name* and therefore became more than a single word—in actuality it became a function. The experimenter asked the question of Lana, via the projectors, by utilizing his own keyboard. The exemplar to be named was held in the experimenter's hand while asking the question.

In this early training, all keys were turned off except for those to be actually used in the training. This left in an active state only the keys for *M&M* or *banana*, *name-of*, *this* and *period*. *M&M* and *banana* were used alternately as exemplars because of their high preference by Lana. Only one exemplar was used at a time, with the key for the unused

one being turned off. Lana was given as much time as possible to make a correct response and was shown the correct sequence by demonstrating it to her as needed. Upon successfully answering the question, Lana was given the item in question and another trial was begun. After this simple response chain had been established, the actual training of the concept "name of" was begun.

(2) *Training*. Training was carried out with the *M&M*, *banana*, *what*, *name-of*, *this* and ? keys turned on, as well as other keys normally on during the day: *please*, *machine*, *give*, *make*, *movie*, *music*, *window*, *open*, *water*, *piece*, *of* and *period*. Two items were used in training so that Lana could acquire a discrimination. The training procedures utilized were essentially the same as in the pre-training phase, although no correction procedures were used and the additional keys were made available for response.

M&M and *banana* were presented in an arbitrary order that seemed appropriate at the time; when Lana appeared to be consistently responding correctly, a test of 100 trials, using *M&M* and *banana* in a strictly random order were given on the next two days. Fifty trials were given each day, with a criterion of 90% correct over the 100 trials being established for movement on to the next phase.

(3) *Transfer Test I*. This was a test of Lana's ability to transfer naming skills for the two objects that she had just learned to an array of five exemplars: *apple*, *chow*, *juice*, *water*, and *ball*. These five items, whose lexigrams were in constant use by Lana, together with *M&M* and *banana* were presented for 10 trials each, with five trials of each item given on each of two days. Together, these seven items constituted a list which was arranged in 10 random sequences, with the additional restriction that the first item in one list was different from the last item in the previously presented list. The question to be asked was, as before, ? *What name-of this*, and again non-correction procedures were used. All items were placed on a plastic tray and held in the experimenter's left hand. Prior to the depression of the *this* key, the tray was lifted to a position in front of the glass door to Lana's room and upon depression of the *this* key, the experimenter pointed to the object in question. If correct on a particular trial, Lana was given the item in question as a reward. If incorrect, a new trial was immediately begun.

(4) *Transfer Test II*. As correct performance on the first presentation of any object would be the strongest evidence that Lana had learned that things in general have names, the second and last transfer test was given. This used the last two available objects in Lana's vocabulary *not* used in the earlier phases of this study, *milk* and *blanket*. Both *milk* and *blankets* had been obtained frequently by Lana through her language system, in a manner analogous to the previously used items. Only two trials were to be given using *milk* and *blanket*, with the items being presented in the same manner as in the previous transfer test.

2. Results

Pre-training

The establishment of the sequence of key depressions "*item-name*" *name-of this period* lasted for four days and 200 trials, half of which were with an *M&M* as the exemplar and the other half with a *banana* as the exemplar.

Training

This phase, involving both *M&M* and *banana* as exemplars, lasted for 12 days and approximately 1000 trials, with between 75 and 100 trials being given per day. A slight

change in procedure was made on the fourth day of this training procedure. Up to this point in the training, Lana was given the item in question as a reward for correctly naming it. At this time, however, she was allowed to choose her own reward by making a request of the system itself for the reward she desired. For example, if she correctly named M&M but wanted a piece of banana, she could "say" *Please machine give piece of banana period* and receive a piece of banana for so doing. It was hoped that this procedure would help keep possible "desires for incentives" on Lana's part from being confounded with the naming task at hand. To keep Lana from making requests during the presentation of a question or after having made an incorrect response, the *please* key on her keyboard was deactivated. If she was correct on a particular trial, the experimenter depressed his *please* key and thus signalled Lana, through the projectors, that a request of the system could be made.

By the thirteenth day of the training procedure, Lana appeared to be responding to the exemplar in question appropriately and therefore she was administered the random order test of M&M and banana on the next two days. On the first day of testing, Lana was 90% correct, missing five out of the 50 trials given. On the next day her performance was worse, resulting in her failing to meet the established criterion of 90% correct over the 100 trials. Additional testing sessions were carried out over the next four days, with Lana's performance deteriorating over those days to the point where she was performing at little better than chance (58%) on the last session.

At this point, the training procedures utilized above were reinstated, but to no avail. Lana's performance had remained essentially at a chance level and she had become increasingly uncooperative—refusing to work at the task and beginning to scream after making incorrect responses. She also stopped attending to what the experimenter was using as an exemplar and by the fourth day of re-training she refused to cooperate at all without considerable verbal encouragement to do so.

As a result of this poor performance on the test trials and the subsequent deterioration of all responding, together with the increase in emotional display, it was decided to move into Lana's room and use her keyboard to pose the questions, with the procedure utilized being essentially the same as before. The only change in procedure was that now Lana could choose her reward from the supply of exemplars that the experimenter had with him in the room, rather than requesting it through the system as before. It was hypothesized that being on a more personable basis with Lana would have a positive effect on her performance. By the third day of this new procedure, Lana appeared to be ready for the more formal test of 100 trials. The procedures used in the previous test were again utilized, only this time the results were more encouraging. Lana achieved the established criterion in the first 100 trials, making only seven errors.

Transfer Test I

Lana was correct 100% of the time on the trials involving M&M or banana, and to a lesser degree on the other items. On individual items, the percentage correct over the ten trials was as follows: Ball, 90%; Apple, 70%; Juice, 70%; Water, 40%; Chow, 40%. However, by dividing the test into sessions (Day 1 and Day 2), one obtains a more optimistic picture of Lana's performance. On the first day (Trials 1–5 of each item), Lana was 60% correct (21 correct out of 35 trials), while on the second day (Trials 6–10 of each item) she was 86% correct (30 correct out of 35 trials). On the first time through

the list of seven items, she correctly named ball (in addition to M&M and banana), while on the seventh and tenth times through the list she was without error.

An analysis of errors made indicated a general pattern, with all but four of the errors being confined to her responding with *M&M* or *banana* for the item in question. Of the four errors not made in this manner, two were identical: she depressed *apple* for *chow*, two items that are vended from the same food dispenser and whose keys were adjacent to each other on the keyboard during the testing.

Another error pattern of interest concerns the items most consistently missed: *chow* (four correct out of 10 trials) and *water* (four correct out of 10 trials). Out of the 19 total errors, 12 were with *chow* and *water*. On the second day of testing, where only five errors were made, four of them *chow* or *water*.

Transfer Test II

Lana correctly named both milk and blanket on the first two presentations of each item.

3. Discussion

The results of the first Transfer Test indicate that not all of the naming process was learned in the training phase, for on the first series of presentations, only one item (ball) was named correctly. That any item was named correctly on the first trial, however, is an indication that something general had been learned during the training procedures. This fact, coupled with her rapid improvement after learning the names of just M&M and banana to the point where she was without error by the seventh presentation of the list of seven items is taken as strong evidence for the learning of the concept "name of" by Lana. Though it took her 1600 trials to learn to name M&M and banana, it took her less than five trials to name the next five items introduced. That she correctly named milk and blanket on the first two presentations of each can be taken as further evidence that she had, indeed, learned the general concept that things have arbitrary names.

Lana had also apparently learned to apply this concept on her own, as the following example will illustrate. Approximately three weeks after the present tests were concluded, Lana was introduced to projected images of other chimpanzees in the following manner: the lexigram key for *slide* was installed on her keyboard and activated, following which the experimenter produced, through his keyboard, the sentence *Please machine make slide period*, at which point a 35-mm slide projector turned on and showed three slides, each for 15 sec. Immediately after the projector had turned off, Lana went over to her keyboard and typed out the following sentence: *Slide name-of this period*, at which point the experimenter said *Yes* through the computer and also rewarded Lana with social praise. Although one observation is inconclusive, that Lana put together a previously established concept with a newly introduced item in a non-required situation, can be taken as some indication of a productive use of the concept "name-of."

That Lana had learned the Yerkish word *this* was in reference to the item in question during the teaching of the concept "name of" can be illustrated by the following examples: *Please machine give piece of this period* and *Please machine give this period*. These two sentences have been said by Lana a number of times, always at night and always when she was alone. That she did not use any of the other new words introduced (*what* or *name-of*) in the same sentence (or any other sentence) and that the use of *this* was appropriate,

although the reference being made is unknown, can be taken as some indication that the word *this* had become for Lana a means of referring to things other than by their names. It also can be reasoned from the use of *this* in the manner prescribed above that Lana was referring to things not present at the time, for if an item was not present at that time the particular key for that item was inoperative. If she had desired something present at the time, she merely had to depress the correct key for it; substitution of the *this* key for an item that is present would gain her nothing. If her desire was for something not present, however, she had no way of making this desire known. The use of the word *this* in the aforementioned manner does seem to indicate some ability by Lana to perceive that which is not present physically.

Several additional and very important benefits have been gained by Lana from this experiment. She has learned to make declarative statements and also to respond properly to the interrogative. By requiring her to answer in the declarative to a question posed to her, she learned that it was possible to use her language system in a manner other than in request for something. She has many times spontaneously given the names of familiar things in her environment without being asked by us to do so. She may have been naming things with the expectation of being able to obtain them subsequently; however, that is admittedly pure speculation.

She has also developed on her own the use of the interrogative marker, in apparent imitation of the experimenter's use of it. For example, she daily will ask ? *Tim move into room period*, to which Tim responds with either *Yes* or *No*. There was no need for her to substitute ? for *Please* in the above sentence, for she had always used *Please* and gained the desired result.

Her use of the interrogative marker, together with the use of the referent "this," adds support to the premise that what is gained from learning a concept, such as "name of," is more than just the concept itself. It is the ability to be capable of expressing oneself that comes as an added benefit from learning a concept. However rudimentary Lana's ability at expressing her thoughts may be at this time, she now has at least some of the basic language elements necessary for meaningful communication. She can correctly reference things by use of their name, she can ask questions, and can apparently substitute a universal (this) for a specific.

Perhaps now her ability to gain the use of other concepts fundamental to language will be enhanced. By building upon a previously established concept, it may be an easier task to teach her other concepts. Results of further attempts will decide whether this premise holds true or fails.

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Christopher E. Parker **The Antecedents of Man the Manipulator**

*San Diego State University,
California, U.S.A.*

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Four individuals of each of ten Primates species were presented with a length of nylon rope and their manipulative responses recorded in detail. The 172 specific types of actions observed were consolidated into 69 generic categories and then further taxonomized into Primary actions, in which the rope was directly acted upon, of two types depending on whether the rope was grasped or not, and Secondary actions, in which the rope was manipulated with respect to objects, with two types depending upon whether the second object was a part of the body or part of the environment.

The ten species tended to fall into two groups: (1) the lemurs, highly arboreal monkeys, and gibbons, and (2) a less arboreal monkey and the great apes. The latter group generally engaged in more different types of actions, more secondary actions, more intentional contacts, more action away from the body, more proximal body contact, and more species-unique actions.

It was inferred from these and other data that the antecedents of Man were more object-interested and manipulative than the precursors of nonhuman Primates at comparable levels of brain size development.

It is becoming progressively more clear that the uniqueness of Man cannot be defined in terms of any one behavioral trait or dimension, any more than the genus could be defined on the basis of any one anatomical characteristic. There is little doubt, however, that many of Man's behavioral characteristics and accomplishments are directly or indirectly dependent upon the manipulation of inedible environmental objects. Therefore, we should increase our efforts to trace the development of this propensity and the rise in the quality of manipulative skills.

The role of inanimate object manipulation as a precursor to tool-using was well recognized at least 20 years ago (Harlow, 1951; Schiller, 1952), and continues to be investigated (Parker, 1969; Menzel, 1970; Shurcliff, Brown & Stollnitz, 1971). Evidence that the degree of interest in inedible, nonsocial objects is related to ecological factors is accumulating (Morris, 1964; Schaller, 1964; Reynolds, 1965; Glickman & Sroges, 1966). The consensus seems to be that the quantity of responsiveness to, and manipulation of, objects is associated with living in a habitat in which the acquisition of diverse foods presents a challenge, and that it may be further increased by relative security from predators. The ubiquitous dimension of relative brain development, especially of the neocortex, is also agreed to be an important factor. Hence, a high quantity and quality of responsiveness is expected in large-brained, omnivorous species living in a broad, often harsh, habitat.

Although there are good data on species differences in the quantitative aspects of responsiveness and manipulation in some Primates (Jolly, 1964; Glickman & Sroges, 1966; Menzel, 1969; Ehrlich, 1970), the qualitative differences have not yet been adequately described or quantified. This would seem to be the appropriate next step and is the object of this and earlier reports from this laboratory (Parker, 1973, 1974).

For the initial attempt, one situation was selected which pilot work had shown would elicit a reasonably high degree of responsiveness in a variety of Primates and which

Table 1**A taxonomy of manipulatory actions****I. Primary Actions****A. Non-grasping contact**

1. Touching without moving the rope (1)
2. Supporting against gravity without movement (2)
3. Raking toward the body with curved fingers (1)
4. Picking at the surface with finger nail (1)
5. Pushing away from the body (3)
6. Moving the BP along the surface (5)
7. Resting on, without moving it (5)
8. Jumping onto the rope (1)
9. Throwing it off the back by bucking the back and/or hunching the shoulders (2)
10. Flipping upwards with rapid finger action, palm upward, little or no arm movement (1)
11. Drawing into the mouth using only the lips (1)
12. Biting with the teeth (1)
13. Licking with the tongue (1)
14. Striking with the BP, a high intensity action (1)
15. Patting or tapping on, a low intensity action (2)
16. Wadding up into a compact ball or mass (2)
17. One hand orbiting the other, with the rope over or around the hands (1)
18. Circular swirling motion with BP on the floor (1)
19. Tossing from open hand to open hand (1)
20. Walking with the rope wrapped around both ankles or with legs in the space between two separated strands (1)
21. Two BPs pushing in opposition to each other (1)

B. Hand grasp plus additional action

22. Picking up off the floor (2)
23. Holding without movement (6)
24. Holding lightly, allowing it to unwind after being twisted (1)
25. Pulling in opposition to the mooring (16)
26. Jerking, a rapid alternate push-pull (2)
27. Throwing, always with a loss of contact at the end of the action (4)
28. Twisting by means of forearm rotation (1)
29. Wrapping around the BP by turning that same BP (1)
30. Mixing up, like tossing a salad (1)
31. Walking about while carrying (1)
32. Pulling by locomoting away from the point of attachment until slack is removed (4)
33. Shaking by a rapid alternation of the direction of movement (3)
34. Waving in a slow alternating or circular motion (3)
35. Rolling, spinning or rocking while holding (4)
36. Two or more BPs pulling in opposition to each other (1)
37. Pulling facilitated by applying another BP to the cage bars to push or pull in opposition to the primary action (3)
38. One BP pulling it taut, another plucking or pushing the taut part (3)
39. Unwinding one or two strands while holding the other two or one (1)
40. Pulling away from the body, hand between the bars outside the cage (1)

II. Secondary Actions**C. With respect to another body part**

41. Draping over another BP, allowed to hang down by gravity (18)
42. Pressing against another BP (2)
43. Holding taut with one hand, turning body to wind rope around body (1)
44. Inverse draping, around BP with ends held up against gravity (3)
45. Sliding across another BP by pulling (3)
46. Pushing into the mouth with another BP (1)
47. Patting rope against another BP (6)
48. Striking another BP with it (1)
49. Rubbing on another BP (3)
50. Forming a loose loop about a BP (1)
51. Wrapping tightly about another BP (11)
52. Forming a circle around the body on the floor (1) and sitting, standing or lying in the circle (3)

D. With respect to an object

53. Rubbing rope on itself (1)

Table 1 (*contd.*)

54. Forming a loop with nothing inside it (5)
55. Wrapping rope around itself (1)
56. Drape over object (1)
57. Squeeze rope and object in same hand (1)
58. Two BPs pulling in opposition with loop around an object (1)
59. Pulling in between two cage bars (1)
60. Pushing out between two cage bars (1)
61. Pushing into a corner of the cage (1)
62. Pressing against an object (3)
63. Rolling rope on floor, back and forth with palm (1)
64. Patting on rope held against an object (1)
65. Striking an object with the rope (2)
66. Rubbing it on an object (2)
67. Smearing feces with it (1)
68. Wadding up under or between objects (1)
69. Forming a loop around an object (1)

allowed for the close observation and detailed recording of manipulatory behaviors. It was also one that allowed simple modification to accommodate body sizes from 18 to nearly 300 lb.

1. Method

The subjects were chosen from those available so as to represent six major taxonomic divisions. There was one pair each of Ring-tailed lemurs (*Lemur catta*) and Black lemurs (*L. macaco*) to represent the Prosimians. The Cebids consisted of Spider monkeys (*Ateles geoffroyi*) and Capuchins (*Cebus capuchinus*). For the Cercopithecoids the Colobinae were represented by Silvered leaf-eating langurs (*Presbytis cristatus*), and the Cercopithecinae by two rather different species, Mona guenons (*Cercopithecus mona*) and Pig-tailed macaques (*Macaca nemestrina*). White-handed gibbons (*Hylobates lar*) represented the Hylobatidae and the Common chimpanzee (*Pan troglodytes*), Lowland gorilla (*Gorilla gorilla*), and Orang-utan (*Pongo pygmaeus*) represented the Pongidae.

There were two male and two female lemurs, four female langurs, and one male and three females of each of the other species, giving a total of 40 subjects. They were born feral and captured at various ages, but had been in captivity for at least two, and some for as long as 15, years at the time of testing. All were maintained under comparable conditions at the San Diego Zoo or at San Diego State University.

The manipulandum consisted of a piece of three-strand nylon mountaineering rope $\frac{3}{8}$ in in diameter for the great apes, $\frac{1}{4}$ in for the rest. One end was secured outside the cage beyond the subject's reach with 5 ft inside the cage for the great apes and 3 ft inside for the others. A figure-eight knot was tied 18 in from the free end. The subjects were not food deprived or rewarded in the test situation. Each was tested individually for 45 consecutive minutes, a duration found earlier to include virtually all of the responsiveness elicited in a single exposure for most subjects. Additional procedural details have been published (Parker, 1973, 1974).

Manipulative behavior was recorded in 111 categories of body part in contact, 173 actions performed, and eight aspects of the manipulandum contacted. The present analysis reports only the actions performed dimension with 172 specific action categories combined into 69 more generic categories on the basis of similarity of action. One category (smell) was omitted because it was a noncontactual action. The 69 generic categories were taxonomized under the superordinate categories shown in Table 1. The numerals

in parentheses in Table 1 indicate the number of specific categories subsumed under each generic category. The major distinction in the taxonomy is between Primary and Secondary actions, defined, respectively as those in which the manipulandum was directly acted upon by the body part (BP) in contact, and those in which the manipulandum was applied to, or used with respect to, an object (including itself). For Primary actions the distinction between (A) non-grasping and (B) hand-grasping actions seemed important, while for Secondary actions the distinction between (C) applying the manipulandum to another part of the body, and (D) applying it to an inanimate object seemed important.

2. Results

Electronic data processing was used to produce a manipulation behavior profile giving the percentage of the total behavior of each subject accounted for by each of the 69 generic categories. A profile of mean percentages for each species was made on the basis of only those subjects in each species group that actually contacted the manipulandum. Subjects not making contact were: three Spider monkeys, and one each of Capuchin, Langur, Macaque, Guenon, and Gorilla. From these profiles analyses of variance and multiple comparisons between species were performed on the per cent of behavior accounted for by each of the superordinate categories in Table 1.

The most salient characteristic of the species profiles was the greater number of behavior categories with a nonzero frequency for the pongids, each category accounting for a lesser per cent of the total behavior.

The next most obvious difference was the relatively greater proportion of behavior classified as Secondary action for the pongids. This is presented in Table 2 in which the species are arranged in descending order on the basis of the mean percentage of Secondary actions. The vertical lines indicate the results of Duncan's New Multiple Range Test. Species not joined by the same line are significantly different from each other at the 0.05 level (left side) or the 0.01 level (right side). In the analysis of variance from which the mean square error for Duncan's test was obtained, *species* was a significant source of variance at the 0.01 level. The multiple comparisons indicated that the pongids performed more actions *with* the manipulandum, as contrasted to actions directly *on* it, relative to the other species, but the difference was significant at the 0.05 level only for the orang-utans and chimpanzees. This difference between the great apes and the

Table 2 Species in rank order for mean percentage of behavior classified as Secondary

Species	%
Orang-utan	35.59
Chimpanzee	28.73
Gorilla	12.81
Capuchin	6.25
Macaque	4.85
Gibbon	3.54
Lemur	2.84
Langur	2.05
Guenon	0.00
Spider Monkey	0.00

others was mainly due to differences in behavior under the D superordinate category, i.e. those in which the rope was manipulated with respect to an object rather than with respect to a part of the body.

For the Primary actions, in which the pattern of significant differences is necessarily identical to those in Table 2 but in reverse rank order, the multiple comparisons indicated very few significant differences among the species within the A and B subcategories.

In summary, the major difference among the species was in the relatively greater proportion of Secondary actions of the type in which the manipulandum is used with respect to objects other than the subject's own body by the orang-utans, chimpanzees, and though not significant, the gorillas.

Actions 22, 23, 25, 36, and 12 were all in the top ten frequency ranks for at least seven of the 10 species. That is, picking up, and then holding, pulling, and/or biting was a very common pattern in this situation.

There are several interesting differences among the species in terms of the ten most frequent action categories. Category 7 (resting on, without movement, including sitting, standing, and lying on) ranked fifth or higher, and accounted for at least 15% of the behavior, for the lemurs, monkeys (except the macaques), and gibbons, but ranked no higher than sixth, and accounted for less than 5% of the behavior, for the great apes and macaques. When these latter species were in contact with the rope it was more likely to be active and intentional, whereas; for the others the rope became in effect part of the floor to be walked on or sat upon indiscriminately. This is further suggested by the relative frequency of category 1 (touching without moving the rope), a relatively nondescript, frequently accidental contact which does not appear in the top ten ranks for the macaques and pongids, but appears in the first nine ranks for all the other species. It accounts for no more than 0.34% of the behavior of the macaques and pongids, but from 2 to 55% (mean = 17.7%) of the behavior of the others.

At one time the action categories were classified according to the direction of movement with respect to the body, but this did not prove to be very fruitful. Yet, category 5 (pushing away from the body) was at least at rank 8 for the capuchins, macaques, and pongids, but did not appear in the top ten ranks for the others, and indeed, in three of the species it did not appear at all and for the other two it was recorded once for each of three individuals (1 guenon and 2 gibbons). In general, actions directed away from the body were rare, but relatively more frequent in the great apes, macaques, and capuchins.

Although the type C actions, manipulation with respect to other body parts, did not differentiate among the species well, one generic category in this group did. Category 41, draping the rope over another body part, appeared in the top nine frequency ranks for the macaques and pongids, but not at all in the behavior of any of the rest of the subjects. Eighteen specific categories were required to describe the ways in which the macaques and pongids, collectively, draped the rope over various body parts. The other species tended to maintain distal, rather than proximal contact.

The remaining differences in the top ten most frequent categories seem to reflect the tendency of the pongids to perform more D type actions.

Action categories unique to one species or to small subsets of species are shown in Table 3. No actions were unique to the lemurs, spider monkeys, langurs, or guenons or to any subsets of these species. In terms of the number of behaviors unique to the species the orang-utans and gorillas were far above the others. The 32 actions unique to the pongids as a group represent 46.3% of the total number of generic categories used for all

Table 3

Action categories unique to various species and species groups

Species	Unique action categories
Orang-utan (O)	11, 24, 28, 39, 53, 58, 67, 69
Gorilla (G)	9, 20, 21, 38, 47, 48, 56, 64
Chimpanzee (C)	57, 68
O & G	18, 29
G & C	15, 43, 44
C & O	14, 30, 40, 42
O, G & C	17, 37, 45, 51, 60
Gibbon (Gi)	19, 49
Gi, O, G & C	6, 10, 59, 62
Gi, C & O	61
Gi & O	55
Macaque (M)	50
M, O, G & C	26, 41
Capuchin (Ca)	63
Ca, G & C	16

the species. Of the 32 actions unique to the pongids, 16 were Secondary actions, reflecting again their greater propensity to perform actions with the rope rather than merely on it.

None of the animals could be said to be fearful of the rope—they either manipulated it or were indifferent to it. Low responsive individuals were likely to pick-up, smell, bite, pull, drop, and ignore the rope. Neither were they fearful of the observer as all were on daily public display. A possibly serious difficulty exists, however, in that some individuals were disturbed by being isolated from the remainder of the social group for the test period and spent a relatively high proportion of time at the door separating them from the group.

3. Discussion

Although the original selection of species was more to survey the six major taxonomic groups than to choose two groups in accordance with any hypothesis, the data do separate the ten species into two fairly distinct sets: (a) lemurs, arboreal fruit and leaf eating monkeys, and gibbons, and (b) macaques and great apes. The former group generally showed less varied behavior, fewer actions in which the rope was manipulated with respect to objects, more undifferentiated (category 1) and less intentional (category 7) contact, fewer actions directed away from the body (category 5), no propensity to drape the rope over parts of the body, and no actions not also seen in the other species.

An important finding here is that manipulation parameters are not predictable from the anatomy of either brain or hand—the anatomy is more similar than the behavior. For example, both the macaque and langur can hold a rope in the hand and place the hand on top of the head, but in this instance one did frequently but the other not at all. Thus, possession of the appropriate anatomy and a high quantity of responsiveness do not guarantee a high quality of manipulation.

The division of the species into two groups on the basis of the quality of actions employed in inanimate object manipulation follows the distinctions made previously by several writers. The two groups represent the specialists *vs.* the opportunists (Morris, 1964). The broad-niched opportunists need a variety of responses adapted to their particular circumstances and a wide variety of potential circumstances in order to capitalize on opportunities as they arise. Such serendipitous exploitation requires the learning in advance of what to expect and do when certain situations arise. The species differed in

their initial repertoires of responses to the object, but more importantly, there is little doubt that after exposure to the manipulandum the species differed in their repertoires of readily available response patterns to (knowledge of) it, should they encounter it again. The alternative way of having a behavior organized and ready before the need arises is to have highly inevitable, species typical behaviors which develop with a minimum of environmental input; but this mode works well only in narrow niches.

Perhaps the single most important aspect of these data is the shift from acting directly on the object (Primary action) to acting with it in respect to yet another object (Secondary action). The trend is clearly discernable in living Primates and must also have occurred in Man's lineage at some point. It is interesting to note that the Australopithecines with brains scarcely larger, and thumbs not much more human, than contemporary pongids, made chipped stone tools, and presumably used other less permanent materials as tools and ornaments to a degree far greater than the present-day chimpanzee (Washburn & Harding, 1970). From this it is inferred that at comparable levels of brain development Man's direct ancestors were probably at least as object oriented and manipulative as the Australopithecines and more so than present day nonhuman Primates and their precursors. It should be noted that this behavioral characteristic has not been predicted from limb anatomy or brain volume or from artifacts, but from laboratory observations on presently living Primates.

All this seems to indicate that the antecedents of Man the manipulator entered an environment and/or niche that made opportunism and learning highly adaptive at a very early stage in their evolution. It is easy to imagine in Man's lineage first and interest in objects of no immediate use, but which, if manipulated appropriately had a high probability of becoming useful, followed by the discovery of behaviors that make the objects make still other objects useful or obtainable, and finally, as suggested by Washburn & Harding (1970), the linguistic naming of these objects so that they could be symbolically manipulated. If the present analysis has any merit, it suggests that the initial stage of the sequence began a very long way back in Man's lineage and represented a major break in behavior between them and the other Primates.

4. Summary

On the basis of the qualitative differences in manipulation represented mainly by the proportion of actions directly on an object as opposed to actions using the object with respect to another object, there was a separation between the lemurs, highly arboreal monkeys, and gibbons on the one hand, and less arboreal monkeys and great apes on the other. The latter were found to exhibit a higher quality than the former.

Since artifactual evidence suggests that Australopithecines were more manipulatively skilled than present day apes with comparable brain volume, it was argued that at comparable levels of brain size, the precursors of Man were more object-oriented and manipulative than the precursors of nonhuman Primates, and that this was a highly significant event in the evolution of Man.

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W. C. McGrew*

Gombe Stream Research Centre,
Box 185, Kigoma, Tanzania

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accepted 12 June 1974

Tool Use by Wild Chimpanzees in Feeding upon Driver Ants

The use of stick tools by wild chimpanzees (*Pan troglodytes*) to feed upon driver ants (*Dorylus (Anomma) nigricans*) is described. Observations of this ant dipping were made over five years in the Gombe National Park in western Tanzania. Chimpanzees find the nomadic ant colonies visually, often re-visiting the subterranean nest sites until the ants move on. The nest is opened manually and tools are made from green woody vegetation. The ant dipping sequence is intricate and efficient. The chimpanzee predator uses several positioning strategies to minimise the ants' massed defensive tactics. Average intakes of 17–20 g/feeding session are estimated. It is concluded that ants may constitute a significant chimpanzee dietary component and that the dipping tools and techniques are relatively stereotyped in form.

1. Introduction

The free-living chimpanzee is now well established as the paramount nonhuman tool maker and user (see reviews in van Lawick-Goodall, 1970, 1973). Each succeeding year sees new records of new types, variations, and locales of tool use (Hladik, 1973; Jones & Sabater Pi, 1969; Nishida, 1973; Rahm, 1971; Struhsaker & Hunkeler, 1971). Behavioural scientists make increasing use of this knowledge to speculate about past hominoid evolution and to examine inter-specific differences. However, to be maximally effective and accurate, such use requires detailed descriptive data collected as systematically as possible. This report presents such observations on one type of tool use exhibited by feral chimpanzees in western Tanzania.

The behaviour described here involves using modified sticks to obtain and eat driver ants (*Dorylus (Anomma) nigricans* var. *molesta* (Gerstaecker)) from ground nests and is hereafter referred to as *ant dipping*. It was first recorded by Goodall (1963), but no detailed description has been previously published for the Gombe chimpanzee population or any other. In addition to her preliminary description of driver ant dipping, Goodall (1963) reported tool use to obtain an arboreal ant species (*Crematogaster* sp.) and a special non-implimental technique to obtain weaver ants (*Oecophylla longinoda*). These occurred in the Gombe National Park, 10 km north of Kigoma. Suzuki (1966) recorded the presence of *Oecophylla* sp. and *Camponotus* sp. in chimpanzee faecal samples from the Kasakati Basin 75 km south-east of Kigoma. Nishida (1973) reported four types of arboreal ants eaten by chimpanzees in Kasoge near the Mahali Mountains, 150 km south of Kigoma. These were *Crematogaster* sp., *Camponotus maculatus*, *C. myromotrema*, and *C. vividus*. The latter three species were obtained with "fishing rod" tools. Reynolds (1965, p. 52) recorded incidental chimpanzee feeding on unidentified arboreal ants in the Budongo Forest, Uganda, but saw no tool use.

In addition, two observers have reported ant eating in groups of chimpanzees released into novel natural habitats. Kade (1967) saw a chimpanzee feed on an unidentified species of ant on Rubondo Island in Lake Victoria. Hladik (1973) recorded chimpanzees

* Present address: Department of Psychology, University of Stirling, Stirling, Scotland, FK9 4LA.

feeding on five ant species, some of which were obtained by tool use, in the Ipassa Reserve Gabon. In some cases, the ants constituted up to 6% of daily food intake.

There has been confusion by several commentators of the various chimpanzee tool use behaviours involved in feeding on social insects, with the tendency to lump these as equivalent (Fox & Tiger, 1971; Oswalt, 1973; Reynolds, 1967). This has been especially true of *ant dipping* and *termite fishing*. The predatory behaviours associated with the different prey species vary considerably in technique and materials, and a future paper will present a detailed comparison of these.

2. Methods

The study population of eastern or long-haired chimpanzees (*Pan troglodytes schweinfurthi*) numbers approximately 60 individuals in two adjacent communities. They live in mixed forest and open woodland habitats on the narrow Great Rift escarpment which forms the eastern shore of Lake Tanganyika. The terrain is rugged, consisting of a series of steep, parallel ridges whose sides form deep valleys, some of which contain dendritic streams. The study area comprises about half of the 70 km² of the Gombe National Park, Tanzania. The Gombe Stream Research Centre has conducted field studies of these free-living chimpanzees since 1960 (see van Lawick-Goodall, 1968, for details).

The chimpanzees are sufficiently tolerant of human beings to allow daylong observation at a range of 5–10 m. Heavy provisioning with bananas initially facilitated this habituation, but since 1968 only selective and infrequent banana feeding has been continued (Wrangham, 1974). Typically an observer and field assistant followed a target chimpanzee and its companions through their daily activities for up to 14 hr a day. The observer dictated into a portable tape recorder a verbal description of the chimpanzee's behaviour and later transcribed this record for analysis.

The driver (or safari) ants, known locally in Kiswahili as *siafu*, are aggressive surface predators which usually move in densely packed columns. These streams, which may function either in emigration or foraging, are of multi-caste constitence and may number several million individuals (Gotwald, 1972). Between emigrations, driver ants build subterranean nests as bases of operation. These are often located in sheltered locations such as under boulders or at the bases of trees and appear to serve as bivouacs.

3. Results

According to examination of faecal specimens, chimpanzees at Gombe eat driver ants at least occasionally during eight months of the year (van Lawick-Goodall, 1969, p. 187). But over a limited period of fieldwork, a single observer usually sees only infrequently the tool use procedure involved in obtaining them. In 45 months of initial observation, van Lawick-Goodall (1968) saw the behaviour only once. Since then observational conditions have improved, and the number of habituated chimpanzees and field workers has increased many-fold. Accumulated standardised records allow long-term data to be compiled. The present report represents 54 descriptions of varying detail of ant dipping recorded between December 1968 and January 1974 and contributed by 18 trained observers. (These are concentrated during 12 months in 1972–1973, during which the author personally witnessed 11 ant dipping sessions.) The data involve 29 different chimpanzees exhibiting a total of 104 feeding episodes at 45 locations. All observations

were fortuitous and did not represent a random sample of the feeding behaviour of the chimpanzee population. What follows is a sequential description of the ant dipping technique, quantified when possible.

4. Finding Ants

Chimpanzees appear to find driver ants visually. Sometimes a moving column of ants is apparent as it crosses an open space such as a path. At other times the disturbed surface of the ground indicates a subterranean ant nest. This is not always obvious, especially in thick undergrowth, and the human observer may see nothing until the chimpanzee orients to it. Nests which have been previously 'worked' by other chimpanzees are more obvious, especially when old dipping tools have been left inserted in them. The soil may be scattered over a radius of up to 1 m, nearby vegetation may be beaten down, and scraps of tool material may be strewn about. If the ants have left such an already-used nest site, the newly arrived chimpanzee usually remains long enough to scrape out a few handfuls of earth as an apparent final check before moving on.

The majority (13 of 17 definite cases) of ant dipping episodes involved chimpanzees re-using nests worked at least once before. (It was impossible for the observer to determine how many times such a nest site had been previously used, which is not to say that the chimpanzees could not do this.) Some discoveries of already-used nests seemed genuinely serendipitous, but others indicated prior knowledge of the location of the nest site. The most obvious example of this involved an individual which made a dipping tool, then walked 75 m without hesitation to an active driver ant nest. One old female with two offspring visited and successfully dipped from the same ant nest four times in seven days. Several times chimpanzees fed at the same ant nest twice in the same day. In most cases, the interval between unobserved previous usages and the observed subsequent use was unknown, but the high re-use percentage implies that the *actual* frequency of ant dipping is considerably higher than the *observed* frequency.

Chimpanzees may also actively search for ants. One female and her offspring in a moving group of chimpanzees passed without stopping by a driver ant column on a main path. Over an hour later they returned alone to find that the ant stream was gone. The female spent the next eight minutes carefully scanning the ground around the path and eventually found the ant nest about 4 m away in thick vegetation. She then dipped from it.

5. Nest Opening

A chimpanzee which feeds from a stream of ants moving on the surface goes directly into tool making after discovering them. One which finds an already-used nest reactivates it by poking into it with any tools left behind by others or by reaching into the hole and pulling out handfuls of soil. Sometimes the latter grades into the opening technique adopted for initially discovered nests: The chimpanzee crouches over the nest site and rapidly and vigourously scrapes at the loose earth with the separated and flexed fingers of both hands (Plate 1). This repeated raking with the finger tips forms a hole of up to 15 cm diameter and depth, out of which the disturbed ants come pouring. Raking may be supplemented by flicking motions of the fore-fingers to clear away stones or other debris. On several occasions chimpanzees ended the sequence at this point, perhaps because insufficient ants emerged.

The opening procedure is often repeated two or three times during a feeding session (9 of 19 cases) either to clear and enlarge the original hole or to open new holes elsewhere on the nest site. On one occasion an adult male used the hole opening motor pattern to feed directly on the ants. He repeatedly pulled out handfuls of soil until he had excavated a hole deep enough to insert his arm to above the elbow (at least 30 cm). From this he withdrew and ate a handful of small white objects, probably ant larvae and pupae. This followed a bout of orthodox ant dipping and was watched intently by the four other chimpanzees present.

6. Tool Making

When previously discarded dipping tools were present at a nest site, chimpanzees used these without further modification on 5 of 13 known occasions. Later, they made new tools, or if at a new nest site, started afresh. The chimpanzee breaks off one or more branches of living woody vegetation, usually from the nearest appropriately shaped shrub or sapling nearby. The potential tool must be straight, sturdy, long, and without side branches. The chimpanzee then pulls off by hand all or most of the leaves or leaflets (Plate 2). In some cases (with rough-barked plant species?) it may further strip off bark by seizing bits at one end of the branch between the lips and pulling longitudinally. The result is a smooth wand averaging 66 cm in length ($N = 13$, range = 15–113 cm) and approximately 1.0 cm in diameter. It was possible to estimate but not measure the initial lengths of a further 30 dipping tools: $\bar{x} = 63$ cm, range = 30–105 cm.

If the tool becomes damaged or coated with soil during use, the chimpanzee may further modify it by biting off worn segments. This occurs in about 50% of cases. Usually it is shortened until it becomes inefficient, then abandoned and replaced by a new one (Plate 3). During a feeding episode, one individual was seen to use as many as six different tools, but the most usual number of tools used per ant dipping episode was two. Sometimes a chimpanzee abandons what seems to be a perfectly good tool and changes to another.

7. Dipping Sequence

With tool in hand or mouth, the chimpanzee approaches the ant nest and inserts the more slender end of the tool into the hole (Plates 4 and 5). The tool is often held with a precision grip in the favoured hand between ball or thumb and side of forefinger. The chimpanzee may release the tool and leave it inserted or move it in a slight swirling motion. In either case it watches carefully until the ants have streamed approximately $\frac{3}{4}$ of the way up the tool, then withdraws it (Plate 6). Most of the ants move up the tool without biting it, giving the appearance of being able to differentiate the inanimate object from the predator.

The hand holding the tool shifts it vertical such that its distal end is just below the mouth. Simultaneously the opposite hand (which may have been idle or supporting in a tripod stance) grasps in a loose power grip the proximal tool end just above the other hand. Immediately the upper hand slides up the length of the tool in a rapid unbroken motion (the 'pull-through') (Plate 7). This momentarily catches the ants in a mass which accumulates on the sides of the flexed thumb and forefinger and lateral surface of the moving hand. The mass is about the size of a hen's egg and contains an estimated 300 ants. As the hand moves up the tool, the mouth opens wide with lips partly retracted.

Plate 1. Opening a driver ant nest by raking with the left hand. The tool is propped against the tree in the background. (Photograph by Stewart Halperin.)



Plate 2. Stripping leaves from a branch to make an ant dipping tool. (Photograph by Caroline Tutin.)



Plate 3. Modifying an ant dipping tool by clipping it with the incisors.
(Photograph by Caroline Tutin.)



Plate 4. Inserting an ant dipping tool into the ant nest.
(Photograph by Caroline Tutin.)



Plate 5. Close-up of tool insertion in ant dipping. (Photograph by David Bygott.)



Plate 6. Monitoring the ants' progress up the tool. The hand holds the tool in a precision grip, and the opposite hand is poised for the pull-through. Photograph by Stewart Halperin.



Plate 7. The pull-through. The mouth is open in readiness and ants from the previous clip are visible in the mouth. Photograph by Caroline Tutin.



Plate 8. Ingesting the ant mass at the end of the pull-through. (Photograph by Caroline Tutin.)



Plate 9. Holding the tool in the foot for the pull-through while suspended above the ground. The right hand and foot provide support against the tree trunk. An old female in the background watches with tool in hand. (Photograph by David Bygott.)



Plate 10. Pausing in the midst of an ant dipping bout to self-groom a foot.
(Photograph by Caroline Tutin.)



Plate 11. Five chimpanzees dip simultaneously from a driver ant nest.
(Photograph by David Bygott.)



As the hand leaves the wand it goes directly to the mouth, transferring the ant mass into it (Plate 8). Presumably the mass of ants is so jumbled that few can bite the predator before being consumed. The chimpanzee's mouth closes and the jaws gnash frantically and exaggeratedly, audibly crushing the ants between the teeth. The ants are then normally chewed and swallowed. The whole sequence from withdrawal to ingestion takes 2-3 sec.

With longer tools the wand may be transferred to and held in the foot (usually the one opposite to the withdrawing hand) while the hand makes the normal pull-through (Plate 9). This occurs in about half of cases (12 of 23) and appears to make the length of longer tools less awkward, and either way the operation seems equally efficient. When a chimpanzee dips directly from a stream of ants moving on the ground, the tool's distal end is placed into their midst, with the tool held diagonally. Chimpanzees may also eat occasional driver ants directly from vegetation with the lips or pick them up between thumb and forefinger and transfer them to the mouth.

8. Positioning

When the nest is disturbed, thousands of ants, each capable of inflicting a painful bite, disperse in active mass defence. From the point of disturbance they radiate out on the ground and up any vertical surface encountered. In seeking to avoid the defenders, the chimpanzee predator uses several strategies. If on the ground it stays as far from the hole as possible and stands bipedally much of the time. Sometimes the chimpanzee will rush forward, thrust in the tool, rapidly retreat out of range, rush forward again when the tool is covered with ants, and then withdraw it and retreat again to eat them. If the tool becomes overwhelmed with large numbers of ants, the chimpanzee may tap it several times to dislodge them from the point of grasping. When the ground becomes thickly carpeted with ants, the chimpanzee pauses periodically to sweep away with its hands the ants from a space around its feet. As the feeding session progresses, the chimpanzee changes its position more and more frequently.

As the ants are concentrated on the ground, the chimpanzee predator seems to prefer dipping from an elevated position (Plate 9). Seventy-four percent of ant dipping episodes involved the chimpanzee moving up off the ground. If a tree trunk is within arm's reach of the hole, the chimpanzee may stand sideways against it, such that only one body-part, the hand not holding the tool, touches the ground. In this case, a foot holds the tool for the pull-through. If shrubs or vines capable of supporting its weight occur near the nest, the chimpanzee will perch on these to dip. Five times chimpanzees were seen to push over nearby upright saplings and use them similarly as perches. (By some definitions, this action would also be considered tool use: an object is repositioned such that the dipping operation is made more efficient.) The ants eventually find their way up to these elevated sites, but fewer reach the chimpanzee at a time than on the ground, and these may be dislodged by vigorous slaps or shakes of the foliage. Chimpanzees also dip from rocks, fallen logs or other raised positions. The ideal situation appears to be a large tree with trunk some distance away but with limbs overhanging the nest site. Suspended from such a limb the chimpanzee can dip with relative impunity. This is not without risk: in one case the tree limb supporting such an individual snapped, and the chimpanzee predator fell directly into the swarming ant nest below.

9. Pauses

An average of 20% of the time spent at the ant nest site is not spent performing the dipping sequence. Four activities which occur during these non-dipping intervals were mentioned above: making new tools, modifying existing tools, opening new dipping holes, and modifying existing holes. However, the greatest number of pauses are spent in self-grooming to remove and eat the biting ants from the chimpanzee's body surface (Plate 10). An individual may abruptly pause for a few seconds at any point in the dipping sequence to do this, particularly from (presumably) sensitive areas such as the face or between the digits. This hasty removal is done with lips or thumb and forefinger, occurring in 23 of 29 feeding episodes. Longer pauses involve moving outside the ants' range to a distance of 5–10 m from the nest and engaging in systematic self-grooming while sitting. This sometimes includes picking the teeth with a finger nail, apparently to clear away fragments of the ants' exoskeletons. These pauses may last for up to 43 min ($\bar{x}$ = 18.8 min, N = 10) and may function to allow the ants to settle down a bit. If a mother has been dipping, she usually rejoins her offspring nearby for social grooming. During pauses the tool is held in hand, foot or groin pocket, or it may be leaned against a tree or left inserted in the dipping hole.

10. Intake

The duration of the average ant dipping episode from arrival at the nest site to departure from it was 18.9 min (N = 72, range = 3–86). The time actually spent in dipping for ants averaged 15.0 min (N = 27, range = 3–48). In the longest bout of ant dipping seen, the author noted every insertion/withdrawal/pull-through sequence over a period of 30 min. These totalled 78, giving a mean dip rate of 2.6 min. It could be argued that this session was atypically long and productive, but if anything it represents an underestimate, as rates tend to decrease over a session as the ants become more dispersed.

It is impossible to count the numbers of ants ingested while a chimpanzee dips. But on another occasion when alone, the author fashioned a tool and dipped a mass of ants estimated to represent a typical chimpanzee dip. The mass was collected intact, killed with carbon tetrachloride and immediately weighed. It contained 292 ants plus some uncountable fragments, in a mixture of castes. (Incidentally this showed that previous attempts on the spot to judge the numbers of ants had been underestimates.) The mass of undamaged ants (N = 225) weighed 0.35 g giving an average dip weight of 0.45 g.

Given (a) rate of dipping, (b) probable number of ants/dip, and (c) length of dipping episodes, one can compute the likely intake of a chimpanzee from an average ant dipping episode: 17.6 g ($= 2.6 \text{ dips/min} \times 0.45 \text{ g/dip} \times 15.0 \text{ min/episode}$). This is only an estimate, but it is probably a conservative one. For example, if the subadults' abnormally brief dipping episodes are omitted from computations, the mean duration of dipping increases to almost 17 min/session, and thus mean intake increases to almost 20 g. Driver ants seem to constitute a significant dietary source of animal matter, probably second only to termites for female chimpanzees (unpublished data).

11. Discussion

Two general impressions emerge from the observations: (1) ants may constitute a significant food source for chimpanzees, and (2) the tool use technique for obtaining ants

is complex and sophisticated. To elaborate on the former point: both Nishida's (1973) and Hladik's (1973) reports and the present one stress that feeding on ants is more common than hitherto suspected. When these results are combined with intake data from feeding on termites (unpublished data), it would seem that insects constitute a small but significant source of chimpanzee nutrition (Plate 11). They probably supply useful animal protein, but biochemical analyses of the constituent nutrients remain to be done. Previous interpretations characterising chimpanzee tool use in feeding on insects as "uncommon" (Oswalt, 1973) or "occasional" (Mann, 1972) would seem to require revision, if these terms imply that it is unimportant.

Regarding the ant dipping technique, it is difficult to imagine a more efficient raw material for the dipping wand than green woody vegetation. Stone, horn, bone or any other natural products have obvious shortcomings such as limited length, heavy weight, brittleness, etc. Since driver ants are nomadic and therefore encountered only fortuitously, the carrying of permanent ant dipping tools would be cumbersome and wasteful of energy. In the Gombe habitat, suitable foliage is always at hand for tool making. In summary, the chimpanzees' ant dipping seems to be optimally efficient although the tool material employed may appear to be the most rudimentary.

Unlike other wild chimpanzee tools which vary greatly in dimension and material, ant dipping tools are very stereotyped. More than any other known naturally used non-human tool, they are shaped to form, presumably based on some kind of cognitive model. A length of about 60–70 cm seems optimal. A tool that is too short would allow too many ants to climb onto the chimpanzee before they could be eaten. A tool that is too long would be awkward to manoeuvre. A tool of too narrow diameter would be floppy and fragile. A tool that is too thick would probably allow too many ants onto the tool at once and make it difficult to form the bite-sized mass during the pull-through. A smooth tool surface is necessary for an unimpeded pull-through. Naturally uniform bark is not a problem, but rough or uneven bark must accordingly be stripped away. Only fairly straight sticks are used: crooks, forks or side branches would slow down the pull-through motion and allow the ants to disperse. The limiting factors outlined above are only inferential, but all relate to dealing efficiently with a pain-inflicting prey which comes in small, mobile units.

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Chicago Zoological Park,
Brookfield, Illinois 60513, U.S.A.

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Wild chimpanzees make and use tools with far greater frequency and variety than wild baboons. Sampling differences; differences in the sensory, motor, or cognitive capacities for skilled tool use; or environmental differences are not responsible. Fortuitous discovery of novel forms of tool behavior probably occurs as rarely among chimpanzees as among baboons. However, research on wild and captive chimpanzees reveals that the discovery is transmitted quickly among chimpanzee groups by observation learning, and thus becomes well-established in the group's behavioral repertoire. In contrast, study of captive baboons reveals that they acquire little information about tool behavior by observation. With little observation learning the behavior is not likely to be acquired by other group members since repeated independent discovery is improbable. Thus chimpanzees' more proficient tool behavior is due mainly to their greater capacity for observation learning. This suggests that the advent of hominid tool traditions was accompanied by a capacity for facile observation learning and thus, perhaps, by language ability.

Savage & Wyman (1843/44) first reported tool use by wild chimpanzees (*Pan troglodytes*) over a century ago. Köhler (1927) and Yerkes & Yerkes (1929), among others, published early accounts of tool use by captive chimpanzees. Nevertheless, the importance of tool behavior in chimpanzee natural history was not appreciated until the extensive field studies of the last decade. I have reviewed this literature elsewhere (Beck, in press) and shall here only note that wild chimpanzees have been observed to throw, brandish, drag, drop, hit, and roll objects during agonistic display; to aim and throw objects; to use objects as clubs, hammers, levers, probes, diggers, and sponges; and to use objects to wipe noxious substances from their bodies. Further, chimpanzees modify objects so that they serve more effectively as tools, i.e. they manufacture tools.

Wild baboons (*Papio* spp.), on the other hand, use tools rarely. In addition to a few second-hand observations (Hornaday, 1922; Kortlandt & Kooij, 1963), Marais (1969) saw wild chacma baboons (*P. ursinus*) hammering tough-skinned fruits with stones, and van Lawick-Goodall, van Lawick & Packer (1973) saw an olive baboon (*P. anubis*) use a stone to wipe sticky fluid from her face and another use a corn cob to wipe blood from his lip. Wild baboons have never been reported to manufacture tools.

Why do wild chimpanzees use tools with more frequency and variety than baboons? Resolution of this question would not only enhance our knowledge of the natural histories of baboons and chimpanzees but also provide increased understanding of the evolution of tool behavior.

The differences between chimpanzee and baboon tool behavior may result simply from sampling differences, i.e. baboons make and use tools at the same rate as chimpanzees but are observed doing so less frequently. This is counterindicated as baboons have been studied more extensively, and under conditions more conducive to observing tool behavior.

A second possibility is that baboons lack the sensory, motor, and/or cognitive capacities to learn to use tools skillfully. This too is counterindicated by the few but reliable observations of tool use by wild baboons (*vide supra*) and by observations of tool use by captives. The variety (although not the frequency) of tool use by captive baboons

approaches that of chimpanzees (Beck, in press). Beck (1972, 1973a) reported that a member of captive groups of both hamadryas baboons (*P. hamadryas*) and Guinea baboons (*P. papio*) learned without training to use a steel rod to secure a pan of food which was otherwise out of reach. Each tool user became quite skilled, often securing the food in less than 30 sec. By their tool use, they each supplied most of their groups' food for about a month. Further, a female in the hamadryas group learned to supply the rod to the tool user (Beck, 1973b) which indicates that baboons even have the capacity for cooperative tool use.

These studies demonstrate that baboons can use tools when the environment makes tool use both possible and reinforcing. It may be that the environments of wild baboons provides fewer opportunities or fewer payoffs for tool use than do the environments of chimpanzees. The best test of this hypothesis is staged in the Gombe National Park where well-studied populations of both chimpanzees and olive baboons occupy the same habitat and compete for many of the same resources. Van Lawick-Goodall (1968, 1970) has described the extensive and varied repertoire of tool behavior of the Gombe chimpanzees. In contrast, prolonged observation of the Gombe baboons, including Ransom's study (1971) of 2500 hr, has yielded only a few cases of tool use.

One contrast in the tool behavior of Gombe chimpanzees and baboons involves aimed throwing in agonistic encounters between the two. Aggression often erupted during competition for provisioned food and during chimpanzee predation on young baboons (Ransom, 1971; Teleki, 1973). Van Lawick-Goodall (1968) observed 20 cases of aimed throwing by chimpanzees at baboons; in 15 cases she judged the thrown object to be large enough to intimidate and in three cases the baboons were hit. Despite the competition and predation, the baboons never threw anything at the chimpanzees.

The Gombe chimpanzees and baboons also differ in the way they feed on insects. During the rainy season, both spend several hours a day catching termites as they emigrate as winged adults from subterranean nests. The chimpanzees, however, are able to expand their exploitation of this food source through tool behavior (Goodall, 1964; van Lawick-Goodall, 1968, 1970). They modify and insert twigs, stalks, and like objects into the termites' subterranean mounds, withdraw the tool, and eat the soldiers and workers which cling to the tool with their mandibles. The chimpanzees are thus able to increase the number of termites eaten and the number of months during which the termites are available. The baboons have no access to termites within intact mounds and thus are restricted primarily to emergent adults. Ransom (1971), however, notes that when baboons opportunistically encounter a broken termite mound they will eat the exposed workers and soldiers, demonstrating that the baboons' failure to secure these forms from intact mounds is not due to inappetence. The Gombe chimpanzees also insert sticks into the subterranean nests and progressions of biting ants and then pick off the attached ants with lips, teeth, and tongue (Goodall, 1964; van Lawick-Goodall, 1968, 1970). Baboons sit on or near the nests and pick up the ants with the fingers or directly with the mouth (Ransom, 1971). This results in apparently painful bites. Ransom notes that mature baboons are not deterred by the bites but his descriptions indicate markedly reduced feeding efficiency.

The baboons' lack of anting and termiting tools is disadvantageous in exploiting these forms of animal protein. This may potentiate their raiding piles of drying fish on nearby beaches where they are subject to aggression from fishermen (Ransom, 1971). The chimpanzees have not been seen to feed on the fish.

While Gombe baboons are competing successfully with the chimpanzees, such observations do suggest selective advantages accruing to the apes by their tool behavior. While compensatory mechanisms may be operative, the paucity of baboon tool behavior cannot be ascribed solely to lack of opportunity or potential reinforcement.

Although wild chimpanzees make and use tools frequently, tool behavior is but a small part of their behavioral repertoire. Thus there are apt to be considerable intervals between incidents. When tools are used to exploit seasonally available resources, months may elapse. This indicates that chimpanzees can recall tool behaviors after considerable periods during which they are not performed. It may be that baboons "discover" tool behaviors as frequently as chimpanzees, but do not recall them when the environment next makes them appropriate. Because of the improbability of "rediscovery", lack of recall would then make baboon tool behavior rare. I thus presented the hamadryas and Guinea baboon tool users (*vide supra*) with the tool task after an interval of one year in order to test their retention and recall of the behavior.

The hamadryas tool user took an average of 42 sec to get the food with the tool on eight trials presented on 3 and 4 December 1970. He again used the tool on 11 December 1970 so that the behavior could be photographed. He then had no access to the tool or the problem setting until 13 December 1971. His respective solution times for three trials presented on that date were 8, 7, and 38 sec ($\mu = 14.3$ sec). The Guinea baboon tool user took an average of 28 sec to get the food with the tool on eight trials presented on 23 and 26 April 1971. With no intervening access to the problem, his respective solution times for four trials presented on 27 April 1972 were 10, 23, 25, and 25 sec ($\mu = 20.8$ sec). These data demonstrate total retention and recall for at least one year. Baboons appear to have recall for tool behavior sufficient to exploit a recurrence of even the most ephemeral seasonal resource. Lack of recall cannot account for the rarity of baboon tool behavior.

In my experiments, baboons acquired tool use by trial-and-error learning (Beck, 1972, 1973a). When the tool was first provided, the baboons initially pulled it into the cage, held it close, and manipulated and explored it ceaselessly. Of course this behavior precluded acquisition of the food since it was positioned outside the cage. Gradually, with habituation to the novelty of the tool and extinction of possessive behavior, the baboons began to push the tool through the cage bars. This was done simply as a variant form of manipulation, not in a purposive attempt to get the food or be rid of the tool. If the tool was pushed or dropped completely beyond the cage bars, it was immediately pulled in. By chance, the tool was finally pushed beyond the food and, when the tool was retrieved, the food was fortuitously pulled within reach. This first solution took an accumulated time of over 11 hr for the hamadryas baboons and 13 hr for the Guinea baboons. With repetition and subsequent reinforcement, both the speed and accuracy of the behavior increased considerably. However, it is clear that initial solution would have been unlikely if the food had been only briefly available and/or if the prolonged opportunity for exploratory manipulation had been precluded by group movement.

Acquisition of tool use by trial-and-error is based on the combination of two conditions which are themselves of low probability: an animal must perform one specific complex response from a large and varied behavioral repertoire and it must do so under the specific circumstances where the response will be reinforced. Undoubtedly, such a combinatorial event is rare in undisturbed wild populations. If baboons are reliant on trial-and-error learning for acquisition of tool behavior, the rarity of their tool use is thus understandable.

Other data from my experiments indicate that this is indeed the case. After procuring food for his group 104 times over about a month, the hamadryas tool user was separated and the problem was presented to the rest of the group. Despite the extended opportunity to observe the tool user, no other group member got the food. Their behavior was indistinguishable from that shown by totally inexperienced animals described above. To maintain group cohesion, the tool user was reunited with the group after only 2 hr. The brevity of the separation and the accompanying social disturbance make equivocal a conclusion that the group learned nothing by observation but the negative result suggested further study.

The Guinea baboon tool user also provided his group's food 104 times over about a month. He was then terminally separated from the group and, after disturbance over his separation had subsided, the tool problem was presented to the rest of the group. Over 21 hr elapsed before another group member got the food with the tool. This solution, like the original solution, also resulted from trial-and-error learning. Thus the prolonged opportunity to observe a skilled tool user did not accelerate the observers' acquisition of the same task. The group touched the tool and touched the food pan with the tool at a higher rate than had occurred during the original learning. This indicates that some information about the task had been transferred by observation. This type of observation learning is known as stimulus enhancement in which the consequences of a demonstrator's behavior in a specific situation influence the orientation of an observer's behavior in a similar situation. In this situation, the animals simply attended more to the tool; it probably became a secondary positive reinforcer due to its previous association with food. One animal imitatively copied a few elements of the tool user's solution behavior but this imitation was too rudimentary to support successful solution.

These experiments with captive baboons demonstrated a very limited capacity for observation learning of tool use, and what did occur was not sufficient to accelerate acquisition of tool use by observers. This is surprising since cercopithecines can learn much about other tasks by observation (Darby & Riopelle, 1959; Hall, 1963; Hall & Goswell, 1964; Kawai, 1965; Kawamura, 1959; Stephenson, 1967). However, van Lawick-Goodall, van Lawick & Packer (1973) also saw no evidence for observation learning of tool use by wild baboons and Vincent (1973) saw none among captive mandrills (*Mandrillus sphinx*). Baboons seem not to be able to acquire appreciable information about tool use by observation. Each must therefore individually learn the behavior by trial-and-error and the probability of such fortuitous discovery is extremely low.

Chimpanzees, on the other hand, learn much about tool use by observation. Menzel (1972) describes the use of branches as ladders by a group of eight chimpanzees living in a large outdoor enclosure. It should be noted that these animals acquired this tool use without training and that Menzel perceptively allowed the behavior to unfold with a minimum of interference. The chimpanzees were found one morning in an observation booth which was elevated on one wall of the enclosure and protected by electric wire. The night break-in was not seen but during the morning most of the animals were observed propping branches against the wall and climbing them to the booth. Two weeks later the chimpanzees learned to stand the branches on elevated runways and prop them against tree trunks to gain access to the treetops which were also protected by electric wires. Within a year the animals were propping branches against the wall of the enclosure and escaping (Menzel, 1973). The first two variations of ladder use were apparently

discovered by one animal and the third by another. Actual discovery was not observed but it seems reasonable to assume that the first break-in was fortuitous. The animals had long balanced branches vertically and climbed and sat on them, frequently holding on to a wall to maintain balance. If a balanced branch had accidentally fallen against the wall, a ladder configuration would have resulted. The second and third variations may have resulted simply from generalization. What is critical in the present context is that on the day after the initial break-in, five of eight chimpanzees had mastered the behavior and two of the remaining three soon became skilled. Seven of the eight animals learned to use branches as ladders to gain access to the treetops within two months of that discovery, and all group members were using ladders to escape within one day of that discovery.

The rapid and nearly synchronous spread of a novel behavior within a social group strongly indicates that observation learning is involved. It is true that each animal could be learning the task individually by trial-and-error but that is counterindicated in this account. The chimpanzees had had access to branches for years before they suddenly used them as ladders. Further, Menzel saw individuals watch carefully as others erected and climbed ladders and then immediately try to reproduce their behavior. Clearly, the chimpanzees more frequently oriented their behavior toward branches, the observation booth, the treetops, and the wall as a result of watching the success of skilled demonstrators (stimulus enhancement) and reproduced, in sequence and with coordination, elements of the topography of the demonstrator's behavior (imitative copying). The information so acquired greatly accelerated the observers' own mastery of the tasks. While some trial-and-error was involved in the initial discovery and in the refinement and perfection of the behaviors, observation learning was of primary importance in acquisition by the group. "Certainly the imitation of each other's behaviors was a more important variable for understanding the performance of the whole group. Once a single chimpanzee performed a given new behavior, others watched closely and attempted the same thing almost immediately; and eventually all members in the group shared the behavior" (Menzel, 1973, p. 456).

Van Lawick-Goodall (1973) specifically discusses the role of observation learning in the acquisition of tool behavior by wild chimpanzees. She notes that young infants watch attentively as their mothers prepare and use tools to secure termites from subterranean mounds. Later they begin to imitatively copy individual elements of their mothers' tool behavior but they do not become skilled until the age of five or six. While trial-and-error is undoubtedly involved in the selection and preparation of appropriate tool objects and in the perfection of the technique, van Lawick-Goodall feels that observation learning "plays a significant role" in the acquisition of this behavior (1973, p. 157).

She also describes a young female watching her mother try (unsuccessfully) to use a stick as a lever to pry an arboreal ant nest from a limb. After watching, the daughter got a stick and did likewise. Similarly a two year old male twice picked leaves and wiped his own clean rump after watching his mother use leaves to clean feces from her pelage.

Van Lawick-Goodall recognizes that these observations are only indications, not proof, of observation learning but her impressions, based on long and intimate study of the Gombe chimpanzees, will probably be supported by fine-grain study of the ontogeny of tool behavior in the population.

If observation learning plays a significant role in the acquisition of tool behavior by wild chimpanzees, intrapopulation variation should be small while interpopulation

variation should be marked. Systematic variations between isolated populations, i.e. tool traditions, indicate acquisition by observation learning. On the other hand, there should be little variation between the tool behaviors of different populations inhabiting similar environments if the behaviors are acquired by trial-and-error.

Of the many wild chimpanzee populations studied, the use of tools to fish termites from subterranean nests has been observed in only a few areas: Gombe National Park, Tanzania (Goodall, 1964; van Lawick-Goodall, 1968, 1970); Kasakati Basin, Tanzania (Suzuki, 1966, 1969); and three of four populations in Rio Muni (Jones & Sabater Pi, 1969; Sabater Pi, 1972). Further, the Gombe chimpanzees use short (15.5–31 cm) stalks, stems, and twigs; the Kasakati chimpanzees use longer (40–45 cm) twigs and pieces of bark; and the Rio Muni apes use quite long (19.5–86.7 cm) sticks. Only the Gombe chimpanzees have been observed to use tools to secure ants from subterranean nests and for this they use relatively long (46.5–77.5 cm) sticks (Goodall, 1964; van Lawick-Goodall, 1968, 1970). However, the Gombe chimpanzees rarely fish for arboreal ants. On the contrary, the Mahali mountain (Tanzania) chimpanzees rarely fish for subterranean ants and termites but frequently fish for arboreal ants (Nishida, 1973).

Several populations have been observed to use hard objects to pound open tough-skinned fruits and nuts. Chimpanzees in Liberia (Beatty, 1951); Central Africa (Savage & Wyman, 1843/44); and the Ivory Coast (Rahm, 1971; Struhsaker & Hunkeler, 1971) use stones for this purpose. Only the Ivory Coast population has been seen to use sticks as well as stones, and to position the objects to be opened in a crevice or depression. The Gombe chimpanzees open tough-skinned fruits by pounding them against trees but have not been observed to hit the fruits with rocks or sticks. Yet Itani & Suzuki (1967) report that Azuma and Toyoshima collected circumstantial evidence that another Tanzanian population does use stones to hammer open fruits.

It appears that there are marked interpopulation differences in tool behavior. The relationship of these differences to environmental differences, e.g. the availability of potential tool objects and the nature of insect nests, and to the geographical isolation of populations, provides a fascinating suite of research problems. The immediately relevant aspect, however, is that the considerable interpopulation variation is additional evidence that observation learning plays a significant role in the acquisition of tool behavior by chimpanzees. A critical experiment would involve translocation of an individual from a population showing one type of tool use to another population which does not. Widespread adoption of the immigrant's behavior by the host group would demonstrate the role of observation learning and would provide a nonhuman model for cultural diffusion.

We can now provide a scenario which accounts for the difference between the tool behavior of baboons and chimpanzees. In the course of undirected exploratory manipulation, an individual chimpanzee fortuitously uses an environmental object to secure a desired commodity or state which was not otherwise available. The subsequent reinforcement increases the probability that the behavior will be repeated and, with reinforced repetition, the behavior becomes more efficient. Thus a novel type of tool behavior is discovered and mastered by one individual. As the discoverer proceeds, other chimpanzees observe. The demonstrator's behavior directs their attention to the critical aspects of the situation and they will imitate elements of his (or her) behavior. Thus they too are likely to gain reinforcement and to repeat and perfect the behavior. The behavior then becomes an established part of the group's repertoire. It is passed to succeeding

generations by the same process (thereby becoming a tradition) and might be carried to other populations by emigrants.

An individual baboon is also apt to accidentally discover a novel type of tool behavior. There are no comparable data from which to estimate the probability of discovery by baboons relative to chimpanzees but my experiments, described above, indicate that the difference is not as great as many intuitively believe. This is not surprising since discovery is based on simple trial-and-error learning, a process which is ubiquitous among vertebrates. As the discoverer repeats and perfects the novel behavior, fellow group members may observe. As a result, they may orient toward critical situational aspects and they may even reproduce rudiments of the discoverer's behavior. However, they acquire so little information by observation that their likelihood of successfully performing the behavior efficiently enough to achieve reinforcement is not very high. Their probes at the situation are thus extinguished and they do not acquire the behavior.

Chimpanzees probably discover a novel form of tool behavior as rarely as baboons. However, because of the ability to acquire information by observation learning, the discovery will be preserved, established, and embellished in a chimpanzee group whereas it will die with its originator among baboons. Thus a researcher sampling a slice of time in the history of a wild chimpanzee population is quite likely to see tool behavior frequently while a study of baboons will yield, at best, a few isolated cases.

This suggests that when enough artifacts are recovered to allow confident dating of the advent of hominid tool traditions, a concomitant capacity for proficient observation learning may be assumed. Further, since language is an unequalled expedient for observation learning, a concomitant language capacity might also be inferred. It is probably not coincidental that chimpanzees, whose skilled tool behavior is supported by facile observation learning, show surprising language ability (Fouts, 1973; Gardner & Gardner, 1969; Premack, 1971; Rumbaugh, Gill & von Glasersfeld, 1973). Observation learning can thus be viewed not only as a critical factor in the development of a rich tool repertoire but also as a vehicle for selective feedback between tool and language behavior.

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Irwin S. Bernstein

*Department of Psychology,
University of Georgia, U.S.A.*

Robert M. Rose

*Department of Psychosomatic
Medicine, Boston University, U.S.A.*

Thomas P. Gordon

*Yerkes Regional Primate Research
Center, Emory University, U.S.A.*

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Behavioral and Environmental Events Influencing Primate Testosterone Levels

A series of experiments demonstrated the influence of multiple environmental and social variables upon circulating testosterone levels in the rhesus monkey. Independent and interaction effects were revealed and a complex model was required to relate the action of these variables to particular measured levels of hormone. The generality of this model is being tested by comparisons with available human data and by extension of the studies to several additional Old World monkeys.

Initial experiments included regularly scheduled sampling from 41 adult and eight juvenile rhesus monkey males. The subjects were maintained in stable or manipulated social groups and studied longitudinally with samples obtained before, during and after each experimental manipulation. The following factors were shown to influence levels of circulating testosterone: (1) ontogenetic status, (2) circadian rhythms, (3) relative access to females, (4) season (seasonal mating typical of rhesus), (5) alterations in social rank and (6) "successful" and "unsuccessful" agonistic encounters.

Attempts to clarify the relationship between behavior and hormones must account for these (and perhaps other) stimulus variables. Although such a model may be highly complex, it does permit some predictive success and appears compatible with available human data. Further comparative studies will indicate the extent to which this model may be extrapolated to humans.

Although we have known for many years that hormones influence behavior and that behavior influences hormones, there has been such a preponderance of effort devoted to elucidation of the first part of the paradigm that in 1965 Frank Beach was moved to write: "... it seems advisable to stress again the fact that endocrine glands which produce secretions that influence behavior are themselves controlled by external and internal stimuli and, that some of these stimuli result directly from behavioral responses" (p. 561).

The influence of gonadal hormones, especially testosterone, on aggressive behavior has been widely studied. The classic model had entailed castration followed by hormone replacement therapy, with behavior studied as the dependent variable. The work of Mason (1969), however, has documented the importance of environmental stimuli in controlling adrenal and other endocrine secretions, and Lehrmann's classic work with the ring dove has clarified the interaction of environmental cues with endocrine secretions (1965).

Whereas most investigators were ready to accept seasonal, diurnal and sexual influences on hormone secretion levels, and readily accepted data showing changed levels in aggressive behavior as a function of hormonal manipulation, few expected agonistic experiences to profoundly alter hormonal levels. Thus, when we first considered measuring the effects of social experience on circulating testosterone levels we approached the problem as one of simple correlation. To this end, our first studies were explorations of possible relationships between a variety of behavioral patterns and measures of plasma testosterone. Behavioral data were collected on a social group of 34 adult male rhesus monkeys (*Macaca mulatta*), an agonistic rank hierarchy was established using directional outcomes in dyadic encounters, and plasma testosterone levels were measured. We did

find significant low correlations for our hormonal measures with (1) status (determined by agonistic outcomes), (2) frequency of aggressive expression and, (3) a general category of "tension" responses including yawning, cage shaking and other nondirected responses of this nature (Rose, Bernstein & Holaday, 1971). No causality or suggestion of directionality was claimed, but we set out to explore behavioral influences on hormones with testosterone levels as the dependent measure.

Our first effort was directed at measuring the influence of sexual access on male testosterone levels; a relationship which we had reasonable confidence in finding, since clear endocrine responses had been shown in female rats (Whitten, 1956), and Vandenberg (1969) had shown that male rhesus monkeys would come into breeding condition if exposed to an estrogen primed female. To this end, we selected four fully adult rhesus males and placed them in small cages to collect baseline data on plasma testosterone levels. Thirteen females were released into a 38 meter square outdoor compound to serve as the "stimulus" condition. The large number of females was thought necessary to insure that at least one would be receptive when a male was introduced. Each male spent two weeks with the females and was then returned to the small cage baseline condition. Blood samples were collected before, during and after exposure to females.

Each of the four normal adult males showed a two or three-fold increase in plasma testosterone levels as a result of introduction to the females, and returned to baseline levels within a few days following removal. An isolation reared male of about the same age was also run in the study and his testosterone levels while with the females could not be distinguished from his baseline (Rose, Gordon & Bernstein, 1972).

We had therefore demonstrated the lability of plasma testosterone levels as a function of one aspect of the social environment, with a rise upon introduction to, and a fall following removal from the females. The data on the single isolation reared male suggested that social history might also influence response to social stimuli and that behavioral events might have longer than just immediate influences on hormonal levels.

The same four males, plus a fifth normal male, then underwent baseline assays in preparation for a different kind of social experience. Each was to be individually introduced to the group of 34 adult male rhesus. We reasoned that the resident males would attack the intruder and quickly overwhelm him, thus tapping into the status and aggression variable identified as correlating with male hormonal levels. "Defeat" was desired, but we did not wish to confound the experience with serious physical trauma, which might maim or kill an animal. We therefore interfered in the attacks whenever we thought serious injury might be imminent, or when it appeared that the introduced animal had ceased resisting attack and become passive. "Defeat," by this definition was achieved in 15 min to 2 hr in all cases. In the follow-up measures of plasma testosterone, the defeated animals all experienced profound drops in circulating hormone levels to an average of only one-fifth of baseline (Rose, Gordon & Bernstein, 1972). The fifth male went into shock and died a few hours after experiencing defeat. This male's wounds were no more serious than those suffered by the other animals, all of which healed with no physical sequelae. Six weeks later, two of the males were each rerun under the female influence condition as a simple replication of the first study.

When the hormonal assays were completed we discovered that, unlike the rapid return to baseline measured upon removal from the female group, following defeat the males continued to show depressed plasma testosterone levels for weeks. This low level of hormone, comparable to that of immature monkeys in some cases, did not, however,

preclude normal responses to females. Within 24 hr of reintroduction both achieved hormonal levels directly comparable to their previous levels with females. In this case, the males showed an eight-fold increase in testosterone levels in order to achieve the same levels as previously. Male responsiveness to female stimulation was thus in no way impaired by the depressed hormonal levels following the single experience of defeat. They were thus not "psychological castrates" despite hormonal levels approximating those of physical castrates.

The dramatic changes in hormonal states as a function of social manipulations had been more than we anticipated, but we noted that our defeated animals had also suffered some physical trauma. We therefore wished to replicate the depression phenomenon while minimizing the confounding influences of injuries. To this end we began baseline sampling on eight subject males and selected a group of seven males as the host group. The host group included: an alpha male who had lost his canines, a second male without canines, and an adolescent male. Using this group not only minimized the physical trauma inflicted on the individually introduced intruders, but in most cases failed to produce signs of defeat in the introducees. Indeed, one introduced male not only successfully repulsed all attacks, but even seemed to achieve some sort of victory over the resident males. The experiment was saved from disaster by the hormonal response of this very successful male. His hormonal levels rose from a baseline average of 950 ng% to over 3000 ng% following his successful self defense. This suggested to us that "victorious" aggression might stimulate the establishment of higher circulating testosterone levels.

Our first experimental test of this hypothesis consisted of measurements of the hormonal levels of resident males who had, or had not, participated in attacking introduced males. We naïvely thought we could distinguish between these two groups, failing to take into account the enormous individual variability in hormonal levels. We now realize that hormonal levels are so responsive to social events that the only practical method of establishing a response to manipulation requires using each animal as his own control. Such before and after testing, comparing post manipulation levels with baselines, is preferable to comparing a "treated" with an "untreated" group inasmuch as individual variability swamps treatment effects in small samples.

Our next efforts therefore included baseline measures of males, and we began a series of group formations and introductions. In the first experiment in this series, four males were introduced to one another and to the previously used group of 13 females. Two of the males actively fought one another and both suffered significant injuries. One became the alpha male whereas the other became the omega. Our hypothesis was verified by their differential hormonal responses. The "successful" male showed a rapid rise whereas the "defeated" male showed a sharp drop. Both males interacted with females, and the defeated male showed a gradual recovery towards baseline over the next six weeks (Rose, Bernstein & Gordon, in press).

This group was then introduced to a second larger breeding group, and was defeated. All four of the defeated males showed profound depressions of plasma testosterone to levels equivalent to those following individual defeat, down to about one-fifth of baseline levels. This time, however, they were not removed from the social group and remained in the company of females. The prolonged depression of hormonal levels thus suggested that "defeat" was a more powerful stimulus regulating testosterone levels than the mere presence of females. The females were not in breeding condition, although some mounting had been observed prior to group merger.

In contrast, the alpha male of the breeding group quadrupled his circulating testosterone level 24 hr after "defeating" the males in the second group. He returned to baseline within the next two days, thus unquestionably responding to the "successful" outcome of his aggression rather than to any change in female availability or social status. He was of course, now alpha over a larger group, but the difference between being alpha over 60 or alpha over 80 does not seem a sufficient change to account for the brief but dramatic surge in hormonal levels. (See Rose, Bernstein & Gordon, in press; and Bernstein, Gordon & Rose, in press *b*, for details.)

Well over 100 additional introductions and manipulations were conducted in this series, and some were directed at isolation of the status variable from aggressive episodes, "victories" and "defeats" (Bernstein, Gordon & Rose, in press *a*). Our simplest procedure was to test the effect of assumption of alpha status by a male following removal of his superiors in his group. Loss of alpha status without "defeat" could be obtained by the return of the original higher ranking males, if they could reclaim their old positions without conflict. In some cases the original alpha male did immediately reclaim his old position without overt aggression. In those cases where we had assayed hormones, we found a rise in circulating testosterone levels following assumption of the alpha position, and a fall following the return of the original alpha male. In this situation we found hormonal response to status changes independent of aggressive encounters, thus suggesting that a change in status alone may be a potent stimulus.

A related series of experiments tested the hypothesis that any male might be manipulated into an alpha or omega position. We attempted to invert the rank relationships in a group of 12 males by individually removing the males and introducing them to five other males. The first male removed and added to the new group was the omega male, and at two week intervals we added the next lowest ranking male from the original group until all of the original group had been introduced to the new group. Inasmuch as seniority in a group is one of the determinants of status, we hoped to invert the relative ranks of the original 12 males in this new group, despite their past history of association. We achieved an immediate success in this manipulation, and only a few individuals varied in their final rank positions by the end of the series. Hormonal responses are not yet analyzed but we should be surprised if this manipulation failed to produce a response inasmuch as both status and aggressive experience were being manipulated as each newly introduced male was attacked by the residents upon introduction.

In a second attempt to manipulate status without significant aggression, or the influence of sexual activity, we had introduced each of six males to a group of females during the nonbreeding season, expecting that the males would claim alpha position with little resistance. Not only did each of the males fail to achieve alpha rank, but in some cases they were chased and harassed by the females throughout the two week experimental period. Two males allowed to stay with ten females throughout the nonbreeding season were successfully integrated into the group only after the onset of the breeding season. Rhesus monkey groups may therefore be more permeable during the breeding season as a result of either behavioral or hormonal changes reflecting the seasonal breeding pattern. The reports of seasonal male mobility by Lindburg (1969) and Neville (1969) for wild troops would appear to support this conclusion.

Seasonal hormonal changes were studied over a 30 month period and clear seasonal variability in male hormonal levels was found. Mean testosterone level for the adult males in a breeding group peaked each fall at about 1200 ng %, and fell each summer to

a low point of 200 ng% (Gordon, Rose & Bernstein, in prep.). In addition, an all male group which could see females across a 7 meter wide open air corridor, but had no direct physical access to the females, also showed hormonal and behavioral changes at the onset of the breeding season equivalent to those of the males living with the females (Gordon, Rose & Bernstein, 1973). A third group of males is being kept in complete isolation from females to see if they will show any seasonal changes in hormones or behavior.

Whereas the all male group in visual contact with females during the breeding season not only could see the females but could witness sexual activity, and could participate in sexual activities with one another, we decided to eliminate the latter two variables by housing males in individual cages with an estrus female caged across the aisle. This will enable us to demonstrate whether distal stimulus properties of the female alone are sufficient to stimulate hormonal response.

In addition to the seasonal rhythmicity noted, and the search for the immediate cues responsible for this rhythm, we identified a powerful source of variation in the diurnal cycle. In agreement with the data obtained from humans (Rose *et al.*, 1972), peak levels occurred during the hours of darkness, but the magnitude of variation may be greater in rhesus where diurnal rhythms matched the magnitude of their seasonal variability. By measuring hormonal levels every 3 hr around the clock, we detected a striking relationship between sunrise and sunset and sharp inflections on the hormonal curve among animals living in an outdoor compound. This suggested a simple light manipulation experiment and five males were maintained indoors where we could shift "daylight" by 5 hr by a light switch timer. After one month we again sampled every 3 hr for 27 hr and initial results suggest that this simple light manipulation did shift the hormonal curve appropriately. Once again the inflection points for both rhesus and human subjects coincide with light changes, albeit in the human subjects "lights out" did not occur until 2300 hours.

Other possible variables which might contaminate our results were also explored, such as simple response to the stress of repeated blood samplings. Happily, our male rhesus show no significant change in hormonal responses as a function of repetitive capture and venipuncture, nor is any influence detectable the day following an extended repeated series of captures and venipunctures. Indeed, cortisol monitoring has demonstrated that simple capture and venipuncture produces little change in experienced subjects, whereas release of isolation reared monkeys into outdoor living areas for the first time may produce marked responses (Bernstein, Gordon & Rose, in press *b*).

We therefore believe we have demonstrated the lability of adult male rhesus testosterone levels as a function of stimuli emanating from the physical and social environments. Multiple variables interact in influencing male hormonal levels, and some of these variables may include long term consequences of early experience. Goy & Resko (1972) using small groups of laboratory animals, demonstrated the importance of prenatal androgen levels with regard to juvenile behavior and it seems likely that differential behavioral histories might likewise influence adult hormonal baselines. As such, an ontogenetic study of play, sexual and agonistic responses was undertaken in groups where the ranks of mothers were known and where maternal androgen levels might also be assayed. As an unplanned bonus, we noted that several infants born to low ranking females were successfully kidnapped by females of higher rank, and are therefore being raised by psychological mothers of high rank after being born to biological mothers of

low rank. After the first year of the study we realized that in order to achieve any generality of findings beyond the rhesus monkey, we would have to extend our studies to other taxa. Groups of stumptails (*Macaca arctoides*), celebes black apes (*M. nigra*), pigtail (*M. nemestrina*), and mangabeys (*Cercocebus atys*) were added to the study of ontogenetic influences, and other cercopithecine groups are also being studied to see if the specific qualities of rhesus social organization and seasonal breeding patterns prevent extrapolation to other species, and any possible generalization to our own hormonal-behavioral feedback system.

Juvenile males show pronounced testosterone rises at puberty (Resko, 1967) and, based on the chimpanzee data of McCormack (1971) and our own behavioral data, we would predict a second increase at the transition from adolescent to fully adult male. We shall also be searching for a female hormonal model which is equivalent to the male model proposed, and we have begun by examination of female androgen levels.

It is tempting, at this point to relate our hormonal findings with rhesus monkeys to what appears to be similar data obtained with humans tested under conditions of stress (Kreuz, Rose & Jennings, 1972; Rose *et al.*, 1969; Rose, 1969). Available comparative data on other cercopithecine monkeys, however, makes us more cautious, inasmuch as some species differences can be detected even in the face of generally similar patterns and ontogenetic changes. Rhesus monkeys show clear seasonal effects; pigtail and stumptail monkeys do not. Juveniles of all species tested have testosterone levels in the same range (less than 200 ng %) but, although adult values overlap, we may find significant species differences. Even seasonal species like the rhesus and crab-eater (*M. fascicularis*) macaques may be six months out of phase with one another (Hadidian & Bernstein, in prep.), although during their respective breeding seasons testosterone levels were comparable (means of 1200 ng % and 1250 ng % respectively). If values from the same months were compared, rhesus values during the nonbreeding season at 350 ng % would have been significantly lower than crab-eater values.

Age effects may not be limited to changes during early development, and this too could complicate comparisons and extrapolation. One aged pigtail male monitored over a seven month period showed testosterone levels in the juvenile range, and yet during earlier years this male had functioned as an alpha and as a beta male with normal adult male behavioral patterns. During his later years, however, he had associated almost exclusively with juveniles, and only shown occasional signs of his earlier adult male activities.

When we attempted to extend our studies to larger Primates we encountered another problem. We assayed hormonal levels of adult and juvenile males of the genus *Mandrillus* but had placed these larger animals under anaesthesia to facilitate handling. The two juveniles at 60 and 210 ng % seemed within the expected range, but the two adult males at 250 ng % and 965 ng % seemed low. The lower value was obtained from the sire of six offspring and he was reproductively active at the time of testing, so we suspect that anaesthesia may influence our measure. Further assays obtained from macaques (*Macaca nigra*) under anaesthesia support our suspicions that the low levels reflected not a species but a drug effect. Eleven samples were obtained from seven adult males in two successive years and the median value obtained was less than 550 ng %. We are, consequently, testing our hypothesis by assaying the same animals with and without the use of various restraining drugs.

With these caveats in mind, we nonetheless feel some justification in further developing

Table 1 **Testosterone mean measures obtained from male macaques**

Species	Classification	Individuals	Samples	Testosterone ng%
Rhesus	mating season adult	7	35	1200
	nonmating season	7	35	350
Pigtail	adult	7	47	955
	juvenile	2	14	165
	aged adult	1	6	160
Stumptail	adult	4	36	1440
	adolescent	1	9	545
	juvenile	1	4	40
Crabeaters	adult	6	6	1250

our model of behavioral, environmental and hormonal variables, and gradually extrapolating our data to additional Primate taxa. We have, to date, analyzed more than 900 samples from 41 individual rhesus monkey males under a variety of experimental conditions. Whereas the testosterone measures obtained averaged about 700 ng %, these cannot be considered as "average" values. Figures for seven males sampled under normative conditions were then selected for comparison with other species. We had to separate breeding season from nonbreeding season data in order to make the comparisons shown in Table 1 inasmuch as most of the species listed do not show a birth season and the only crabeater macaque data were collected early in their breeding season.

The hormonal levels showed considerable month to month variation for each individual but as with our initial rhesus studies, we had also collected data on frequency and direction of agonistic response elements as well as other social responses. We will test for correlations between each of these and relative hormonal levels. In our initial rhesus study we had demonstrated a small but significant correlation between hormonal levels and social rank, with a sample of over 30 males. In our pigtail, crabeater and stumptail groups we had only four to six adult males in each group and it was therefore not surprising that we failed to find significant correlations between agonistic rank and hormonal levels. It may be of interest to note, however, that in each of these three groups the alpha male did have the highest mean testosterone level.

We must, of course, not neglect the other end of the feedback loop. Hormonal influences upon behavior have certainly been amply documented, although we might heed Rowell's remarks (1973) that the influence of hormones on behavior is most readily demonstrated in restricted social settings and becomes less and less obvious as the complexity of social grouping increases. Thus, Mirsky's (1955) failure to produce changes in status as a function of testosterone injections in his groups of rhesus monkeys does not preclude hormonal influences on behavior. Instead it warns us that we may have to search for more subtle mechanisms.

Pilot work in our laboratory included administration of human chorionic gonadotropin to two males in a group of eight. Neither male showed any change in rank or aggressive response frequency, but we noted an increased incidence of wounds suffered by the males. Thus, the measured testosterone responses in excess of 7000 and 8000 ng % were expressed behaviorally in a manner too subtle for us to detect, but recognized by the other animals in the group such that they invoked social mechanisms designed to maintain the established social organization.

A number of environmental and social variables significantly influence male testosterone levels in the rhesus monkey. We have demonstrated significant influences for each of the following factors: (1) season (possibly mediated by changes in distal cues emitted by females), (2) circadian rhythms (possibly mediated by light-dark transitions), (3) access to or separation from estrous females, (4) changed social status (measured by directionality of agonistic encounters), (5) "successful" and "unsuccessful" agonistic experiences, and (6) ontogeny. Additional factors which may influence gonadal secretions include: past social history, general health, physical trauma, and separation from or return to social partners.

We are still investigating the relative influences of each of these variables and their interrelationships, but it is already clear that some factors may at times completely overshadow the effects of others. For example, "defeat" and "victory" may overshadow the effects of introduction to receptive females, and changes in status may produce profound hormonal alterations despite the continued presence of sexual influences. Each of these three variables has been demonstrated to have an influence independent of the others, and all of them certainly override the effects of physical trauma. We have not yet explored the interrelationships between these social factors and potent environmental variables such as circadian and seasonal cycles.

The multiple variables already shown to influence testosterone levels precludes any simplistic accounting for a particular hormone value. Rather, an acceptable model will require appropriate controls and longitudinal study. Such an approach may explain the variability obtained in hormonal measures. For example, mid ranking males in stable social groups may show wide fluctuations in testosterone level as they experience successes and rebuffs in rapid sequence. Considering the number of possible interaction effects, it is not surprising that most of the available data relates to single or paired animal manipulations.

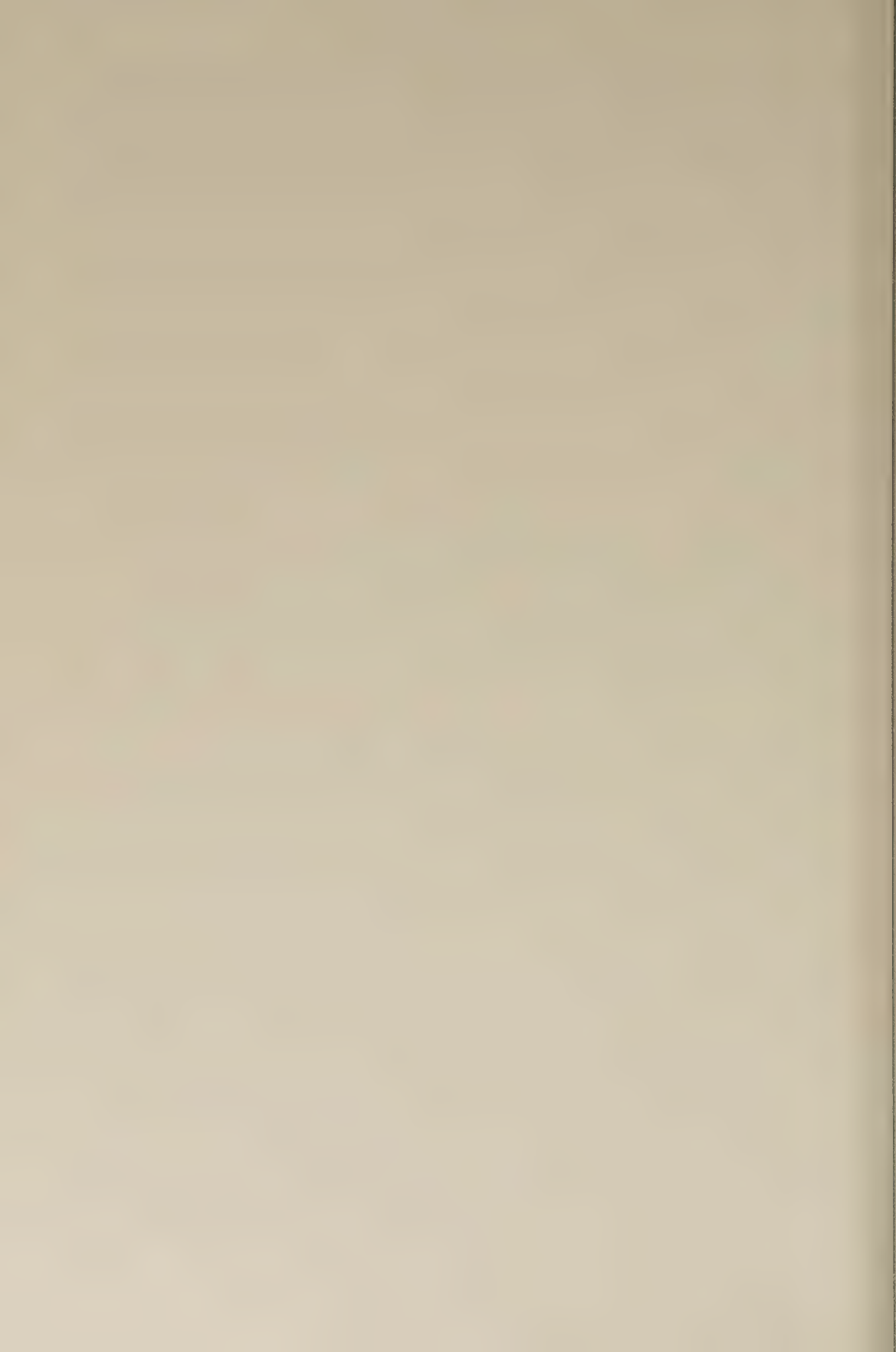
We must, therefore, seek to refine our measurement techniques so that we will be able to detect the behavioral subtleties, and better identify the mechanisms involved in maintaining social relationships. Changes in these relationships may profoundly influence hormonal secretion. Verification of this hypothesis in a number of primate taxa would then permit cautious application of these theories to human behavior and clinical practice.

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Stephen J. Suomi*
Harry F. Harlow
Melinda A. Novak†

University of Wisconsin,
Madison, Wisconsin 53706, U.S.A.

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Reversal of Social Deficits Produced by Isolation Rearing in Monkeys

A major body of research has clearly demonstrated that rearing monkeys for at least the first 6 months of life in total social isolation from conspecifics produces profound psychopathology, including both massive social deficits and ideosyncratic self-directed behaviors rarely seen in normal monkeys. Previously, isolation-induced psychopathology was thought to be permanent, and various theoretical explanations, e.g. critical periods and "emergence trauma" were posited to account for such phenomena. Recent research at Wisconsin has indicated that the isolation syndrome in monkeys is, in fact, reversible, rendering the above theoretical positions inadequate. In this paper, the procedures for successful rehabilitation of isolate-reared monkeys are described and an alternative theoretical explanation presented. Implications of the theory and data are discussed.

The notion that social behavior of an organism is greatly influenced by early social experience is not entirely foreign to behavioral scientists. The idea is central to the ethological principle of imprinting, forms the basis for social learning theory in developmental psychology, and provides the justification for psychoanalytic interpretation of adult personality and psychopathology as a function of infantile experiences. Clearly, early social experience is viewed as critical to subsequent social development by a large number of investigators in diverse fields of inquiry, and not surprisingly, experimental studies of early rearing environments permeate both the human and the animal literature.

The field of Primate social behavior and development hardly provides an exception to the above emphasis. At the Wisconsin Primate Laboratory, study of early social development has been carried out extensively for almost 20 years. Two basic strategies have prevailed, the first involving identification of variables which affect exhibition of role-like behavior among monkeys of different age and sex categories. For example, research utilizing artificial surrogate mothers has demonstrated *contact comfort* to be the primary variable of importance in early mother-infant attachment, with temperature, feeding, and motion secondary but still significant variables (Harlow & Suomi, 1970).

The second approach to the study of early social experience has involved rearing infant monkeys in a variety of social environments and studying both immediate and long-term consequences of such rearing. Babies have been raised in environments which range from partial or total isolation from conspecifics (Harlow & Harlow, 1962) to nuclear families which permit unlimited interaction with family and friends of all ages and sexes (Suomi, 1972). The results from these researches have been both consistent and clear-cut: the more restrictive the early social environment, the more deficient will be the monkey's social behavioral repertoire.

Without question, the most impoverished social rearing environment to be studied extensively at the Wisconsin laboratory has been that of *total social isolation*. Here, monkeys are separated from their mothers immediately following birth and are placed in

* Requests for reprints should be addressed to Dr Stephen J. Suomi, University of Wisconsin Primate Laboratory, 22 North Charter Street, Madison, Wisconsin 53706, U.S.A.

† Presently at the Departments of Zoology and Psychology, University of Massachusetts-Amherst, U.S.A.

total isolation chambers, $2.5 \times 2 \times 2.5$ ft metal-incased enclosures which effectively deny a subject any visual or tactual contact with any social agents (Rowland, 1964). Diffuse light is provided to the incarcerated subjects in order to prevent optical nerve degeneration (e.g. Riesen, 1960), and food, water, and milk preparations (Blomquist & Harlow, 1961) are delivered to the monkeys within the chamber itself. Thus, animals housed in the chambers are subjected to minimal physical but maximal social restrictions.

We have studied for almost 15 years the consequences of rearing monkey infants in total social isolation, and, in a word, they are devastating. Subjects so reared for at least the first 6 months of life exhibit a wide range of bizarre, self-directed behaviors upon removal from isolation. Such behaviors are seldom, if ever, displayed by monkeys reared in more charitable social environments. More importantly, monkeys emerging from social isolation display a marked absence of virtually every social activity characteristic of socially normal animals. When placed with each other they are worse than wallflowers (see Plate 1), as they shun social contact and instead withdraw to the extremities of the test area. When placed with socially competent age-mates they manage to elicit intense and continual aggressive attacks (see Plate 2), which does not tend to improve their social activity.

Aggression, however, is not entirely foreign to the social isolates' behavioral repertoire. It is merely inappropriate and usually ill-directed when it does appear later in the isolates' lives. For example, a monkey reared for the first 6 months of life in total social isolation may, as an adolescent, repeatedly attack a helpless infant, something no normal monkey would do. Or, such an isolate may attempt to attack a large, dominant male, something few normal monkeys are foolish enough to attempt, at least more than once. A psychiatrist might call it masochism.

If aggression in isolate monkeys appears faulted, sexual endeavor is simply fruitless. Procreation is deemed virtually impossible and recreation improbable by the isolates' sexual inadequacies. Procreation via artificial insemination is possible. However, in view of the results it seems hardly advisable. Isolate females are inept sexually, but their maternal competence is even more sad and sorry (see, for example, Plate 3).

Severity of psychopathology has been found to be directly related to duration of isolation immediately following birth. Data from numerous studies clearly verify that 9-month isolates are more debilitated than 6-month isolates, while 12-month isolates are virtual social vegetables. To further complicate matters, individual behavioral differences among "similarly-reared" isolates are enormous, not so much in terms of severity as in terms of diversity. Self-directed activity dominates the repertoire of almost all isolates, and the form of activity tends to be most ideosyncratic.

The debilitating effects of total social isolation were once thought to be not only perverse but also permanent. At the very least, the isolation syndrome has proven to be exceedingly resistant to change, by either behavioral or biochemical therapeutic regimes. For example, Sackett (1968) attempted to shape social contact initiations of isolates toward other monkeys via an aversive conditioning paradigm, but his results were unspectacular within the tight constraints of the conditioning situation and showed little, if any, generalization to other social situations. Mitchell & Clark (1968) tried to minimize postulated "emergence trauma" following removal from isolation, i.e. the shock of coming from a sterile environment into one comparatively rich in social and nonsocial stimulation, by adapting their subjects during the isolation period to the specific physical environment the monkeys would encounter in social interaction after isolation. However, such

Plate 1. Monkeys soon after removal from isolation.

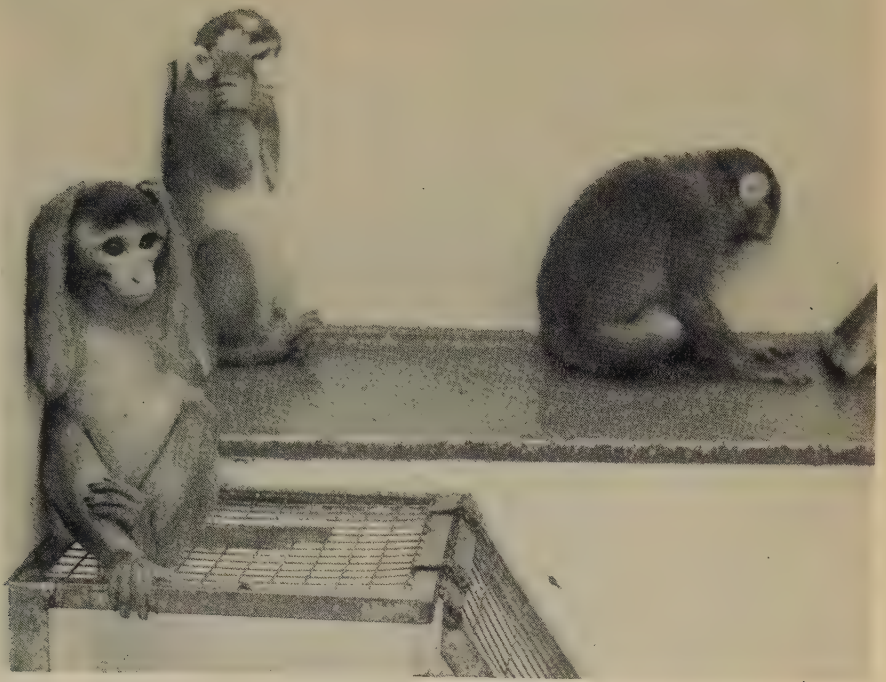


Plate 2. Normal peers attacking isolate-reared age-mates.



Plate 3. Isolate female crushing her infant into wire-mesh floor.

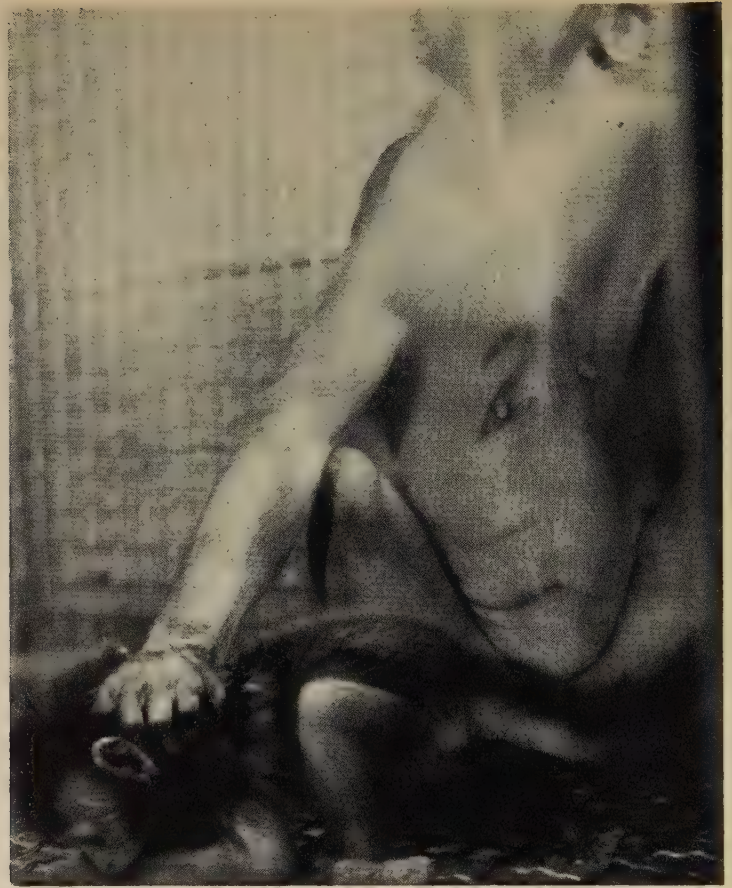


Plate 4. Initial response of isolates to therapists.



Plate 5. Therapist clinging to back of isolate.



Plate 6. Isolate (above) reciprocating play initiated by therapist.



procedures did not significantly enhance the social performance of their isolation-reared subjects. Taking a related approach, Sackett (1966) and Pratt (1969) exposed infants to slides of other monkeys during their tenure of isolation. Again, the effects this manipulation had on subsequent social performance by the isolates appeared to be minimal. In summary, these efforts designed to alleviate the devastating consequences of isolation-rearing were generally unsuccessful, underscoring the view of many researchers that deficits produced by isolation-rearing were irreversible, albeit permanent (Harlow & Harlow, 1962; Sackett, 1965; Harlow & Harlow, 1965).

Despite the apparent consistency of findings regarding the effects of isolation-rearing in monkey subjects, several differing theoretical explanations for the data have been posited by various investigators. Among these is the *critical period* hypothesis (e.g. Scott, 1962), which postulates that the young of most social species pass through chronological periods during which certain social input is *necessary* for adequate subsequent social development. The implications of the theory are that animals denied appropriate social input during a critical period will exhibit permanent social deficits independent of subsequent social stimulation. If one views the first 6 months of a monkey's life as a critical period, the data to date appear quite consistent with the theory. An alternative explanation of isolation effects has involved the previously-mentioned notion of "emergence trauma." Here it is postulated that animals reared in sterile environments perceptually develop low tolerance for complex stimuli, and when they are suddenly transferred to a "normal" environment they withdraw to avoid, as much as possible stimulus input. The notion that isolate-reared monkeys avoid complex stimuli has received considerable empirical support (Sackett, 1970; Pratt & Sackett, 1967), while an impressive body of canine research has been consistent with the theory's predictions (Fuller & Clark, 1966).

Nevertheless, we at Wisconsin believe that the above theoretical positions provide inadequate explanations of Primate isolation data. We are the first to admit that rhesus monkeys are maximally responsive to certain social stimulation during specific chronological periods. Further, the notion that behavioral change accompanies major shifts in social environments has been substantiated by a large body of our own data. But while critical period theory may identify a crucial chronological span (e.g. the first 6 months for rhesus monkeys), it does little to specify the mechanisms involved in actual development of aberrant behavior. Moreover, data from several studies of learning capability have consistently failed to yield any evidence of intellectual deterioration during isolation rearing, raising the possibility that isolates could be taught appropriate social behaviors given the proper stimulation (Harlow, Schiltz & Harlow, 1969; Gluck, Harlow & Schiltz, 1973). With respect to emergence trauma, data collected *during isolation* clearly show that most patterns of disturbed activity are predominant features of the isolates' behavior repertoire *prior* to emergence, and that levels of these behaviors return to baseline within a month following removal from isolation (Suomi & Harlow, 1972; Harlow & Novak, 1973).

We prefer to view aberrant isolate monkey behavior as a form of learning deficit. Extensive study of normal social development in monkeys has convinced us that while components of social behavior may have unlearned antecedents, most sophisticated social activity is acquired only through prolonged physical interaction. Play, sex and aggression do not suddenly emerge full-blown, but rather are developed and integrated into existing and developing repertoires gradually. Isolates, denied the opportunity to

learn through physical interaction with conspecifics, do not spontaneously exhibit sophisticated social behaviors when they are eventually exposed to other monkeys.

Confounding the problem of lack of opportunity for social learning is the behavior repertoire that the isolates *do* learn during isolation. Born with the reflex of clinging and having no mother, surrogate, or peers with whom to cling, the isolates learn to cling to themselves and thus develop self-clasping behavior. Born with the reflex of sucking but denied a maternal nipple for nutritive or nonnutritive contact, they learn to suck their own digits and thus develop high levels of self-orality. Responsive to motor feedback but lacking a source of mobile stimulation, these monkeys provide their own motion and thus develop stereotypic activity. Developmental plots of the occurrence of these self-directed behaviors resemble traditional learning curves (Suomi & Harlow, 1972).

With these points in mind we have, over the past 5 years, initiated several researches explicitly designed to reverse the behavioral effects of isolation-rearing. Our strategies have had two approaches: (a) to reduce or eliminate patterns of self-directed behavior not seen in socially competent animals and (b) to replace such patterns with social activities gradually increasing in complexity and sophistication. We have always assumed that the extent of isolate rehabilitation obtained would be a function of the degree to which both these were realized.

The initial study (Suomi, 1973) had as its purpose only *partial* rehabilitation of isolation-reared monkeys, specifically, reduction of self-directed abnormalities without concomitant development of elaborate social repertoires. Monkeys were reared for the first 6 months of life in total isolation, then placed in individual quadrants of a quad cage (Suomi & Harlow, 1969) for a 2-week period in order to assess postisolation behavioral levels. These were found to be typical of 6-month isolates from previous studies, with high levels of self-mouthing, self-clasping, rocking and stereotypy and with low levels of locomotion and exploration. At this point the isolates were given heated simplified surrogates, which previous research had demonstrated to possess the capability to promote acceptability of physical contact and development of security in infant monkeys (Harlow & Harlow, 1965; Harlow & Suomi, 1970).

Initially, the isolates avoided the surrogates. However, in subsequent stumbles about their cages they inadvertently contacted the surrogates and, presumably, learned that the surrogates were not threatening but rather soft and warm. Soon, the isolates freely clung to the surrogates and incompatible self-directed behavior such as self-clasping and stereotypy declined significantly. Shortly thereafter the isolates began to spend significantly more time moving about and exploring their cages when not on the surrogates. Apparently, introduction of the surrogates promoted contact and security in these 6-month monkeys, just as previous researchers had demonstrated in neonatal subjects. Correspondingly, aberrant behavior declined.

The subjects were then housed together in pairs, along with their surrogates. Self-directed behavior continued to decline and locomotion and exploration continued to increase. Partner contact steadily increased over an 8-week period, and primitive play emerged in most subjects. However, this was as far as recovery progressed. Play was retarded, in both form and frequency of occurrence, even after prolonged partner exposure and new housing with other monkeys. Appropriate sexual behavior failed to appear. In short, the isolates remained unsophisticated in their social behavior (Cummins, 1973).

These results were entirely predictable if one views development of complex social

activity as a learned product of interaction with competent conspecifics. Being inanimate, surrogates cannot initiate social interactions and fellow isolates could hardly be considered to be competent playmates. However, the study did indicate a plausible strategy for elimination of self-directed activity: development of contact acceptability. What remained for complete rehabilitation was development of procedures to insure adequate learning of appropriate social behaviors.

Here, the substantial backlog of normative development data accumulated over the past 12 years proved invaluable. Aggression is routinely administered to strangers by competent subjects at 7 months of age. Since the behavior of isolates is indeed strange by normal monkey standards, it is not surprising that previous studies reported extensive aggression against and no recovery exhibited by isolates exposed to competent age-mates. Further, by 7 months of age well-socialized macaques have complex behavioral repertoires, characterized by highly active and extensive play bouts. It is no wonder that isolates seem overwhelmed by the behavior of competent peers.

However, well-socialized monkeys are *not* aggressive nor do they possess a highly complicated social repertoire *earlier in life*. For example, in normal 3-month-old monkeys aggression has not yet matured and simple play patterns are just beginning to emerge. Moreover, such monkeys still cling actively to other social agents, although such behavior soon disappears. Given these qualifications, it seemed plausible that 3-month-old monkeys might be appropriate social stimuli for helping isolate-reared monkeys develop adequate social repertoires, and so we ran a study using such monkeys as "therapists" (Suomi & Harlow, 1972).

Monkeys were reared for the first 6 months of life in total isolation, then they were individually housed for postisolation behavioral assessment for 2 weeks as above. At this point they were permitted to interact with 3-month-old socially-normal "therapists" for approximately 8 hr per week. Interactive sessions continued for a period of 6 months.

When first exposed to the therapists, the most common reaction of the isolates was to seek out a corner and rock and self-clasp (Plate 4). The most common reaction by the therapists was to cling to the isolates (Plate 5) not an unusual response inasmuch as clinging was at this chronological time the predominant social behavior shown by the 3-month-old monkeys. With respect to providing a soft and warm surface, the therapists did not greatly differ from the heated surrogates employed in the previous rehabilitation study (Suomi, 1973), and the consequences for the present isolates were similar: development of contact acceptability, reduction or elimination of self-directed behavior, and increases in exploration and locomotion.

Unlike the surrogates in the previous study, however, the present therapists could both interact and develop socially. By the time they reached 4 months of age, play behavior superseded clinging in these monkeys, and by 8 months of age it was the dominant feature in their social repertoire, just as it is in most normal 8-month-old monkeys. To our delight, the isolates developed their social repertoire in parallel with the therapists: when the therapists clung, they clung back, and when the therapists played, they played back (Plate 6). By the end of the therapy period the isolates and therapists were hardly distinguishable in terms of levels of both social and nonsocial behaviors. As such activity generalized to other social situations (Cummins, 1973), social rehabilitation appeared to be complete. Suomi & Harlow (1972) pointed out that these results were quite inconsistent with both critical period and emergence trauma explanations of isolation effects, but well in line with learning deficit considerations.

In a more impressive study of isolate rehabilitation, Novak & Harlow (in prep. *a*) reared monkeys in total social isolation for the first 12 months of life before subjecting them to a therapeutic procedure similar to that described above. The 12-month isolates were far more debilitated than are 6-month isolates (Rowland, 1964), and Novak altered her procedure accordingly. Isolates were first permitted visual interaction with each other, then self-paced visual interaction with the therapists, and then physical interaction with each other before they were finally physically introduced to the younger, socially competent therapists. Formal therapy continued for 6 months.

As in the Suomi & Harlow study, remarkable recovery was displayed by Novak's 12-month isolates. By the end of the therapy period isolates and therapists did not differ significantly in levels of play, social contact, exploration and locomotion while levels of self-clasping, rocking and stereotypy were low in both groups. Novak & Harlow (in prep. *b*) continued to test these isolates formally until the monkeys were $3\frac{1}{2}$ years of age. The impressive recovery shown by the isolates did not regress over time. Rather, by adolescence these subjects were actively interacting with other monkeys, formed stable and well-established dominance hierarchies with a minimum of inappropriate aggression, and displayed more than occasional acts of appropriate sexual behavior. We are presently waiting for babies to arrive.

We view the implications of these research findings with isolate monkeys as far-reaching. First, they should put to rest the critical period notion that social deficiencies developed in impoverished environments early in life are necessarily permanent and irreversible. It is true that spontaneous recovery rarely, if ever, occurs in an isolate. However, as the present data demonstrate, rehabilitation is not impossible—although it does require considerable time and effort. If these data generalize to Man, then it is possible that the role of early experience in adult social activities may not be as important or permanent as suspected by current theory. More importantly, it raises the hope that exceedingly sterile environments, e.g. foundling homes in the early 1900's, may not necessarily have permanently adverse effects if suitable subsequent environments can be found.

But it must be remembered that rehabilitation of isolates is no easy or rapid task. Procedures which focus merely upon elimination of self-directed abnormalities are not likely to yield sophisticated patterns of social behavior. Procedures which focus exclusively upon elicitation of appropriate social activity without attacking thoroughly entrenched patterns of self-directed behavior are likely to result in withdrawal from stimulus overload and possible increases in the undesirable behavior patterns. Instead, a social environment conducive for learning basic antecedents of complex social behavior patterns must first be provided, followed by social stimulation sufficient to enhance social development. In this case a knowledge of normative patterns of social development is essential to successful rehabilitation. Some current therapeutic efforts with human child schizophrenics are utilizing similar procedures (Schulsinger, 1974; Hartup, 1974), although we are the first to admit that the isolate monkey is probably not an adequate model for most human schizophrenias.

Nevertheless, we believe that the general approach involved in the present use of monkey therapists may have utility for some human psychopathologies. Unlike most human therapists, there was little to differentiate these animals from an ordinary population of socially normal monkeys. They had received no prior training in clinical theory or practice, but rather rehabilitated the isolates simply through exhibition of the behaviors which have characterized the social development of normal monkeys for thousands of

years. And, they were effective therapists. We are currently using a similar strategy, i.e. selecting certain monkeys for use as therapists on the basis of the normative behavior patterns they exhibit, to rehabilitate monkeys who have been experimentally depressed (Harlow & Suomi, 1974). Their disorders differ from the isolation syndrome and hence we are using different therapists; not younger peers but rather slightly older, very active and playful peers.

The choice of social therapeutic environment must depend upon the nature of the disorder, if therapy is to succeed. With respect to human therapy, much effort to date has been directed toward individual (and often intellectual) interaction between patient and professional therapist, with less consideration given to the social environment the patient encounters when he leaves the therapist's office. It is conceivable that human professional therapy can be augmented by exposure of patients to appropriately chosen nonprofessionals whose daily activities provide a social environment conducive to rehabilitation.

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Harmut Rothe

*Institute of Anthropology,
University of Göttingen,
34 Göttingen, West Germany*

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Allogrooming by Adult *Callithrix jacchus* in Relation to Postpartum Oestrus

The allogrooming behaviour of the parents (= α -animals) of three family groups of *Callithrix jacchus* has been studied during 25 days following birth. A total of 22 postpartum periods has been analysed. We recorded significant increase of grooming activity beginning with the 5th day postpartum. Allogrooming initiated by invitation gesture dropped to one-tenth of the total allogrooming frequency within one week, starting from day 5 postpartum. As a rule, allogrooming activity increased abruptly, whereas the decrease was mostly continuous, lasting several days. The maximum of postpartum allogrooming frequency preceded to some extent the maximum of copulatory activity and sexual willingness of the ♀. The ♂ made more attempts to groom the ♀ than vice versa. Up to the 18th day postpartum the ♀ ♀ ended more grooming sessions than the ♂ ♂ and than during anoestrus. The ♀ ♀ refused more invitations to grooming than did the ♂ ♂. The analysis of postpartum grooming behaviour in *C. jacchus* does not allow for accurate determination of the first and last day of the postpartum oestrus.

1. Introduction

Neither regular and clearly detectable cyclical changes of the genital region (e.g. swelling of the circumgenital skin) nor cyclical menstrual bleedings are to be seen in the marmosets (Epple, 1970; Hampton, Hampton & Landwehr, 1966; Langford, 1963; Lucas, Hume & Smith, 1937; author's observations). Russell & Zuckerman's (1935) and Reichenbach's (1862) observations as to the occurrence of a 'sexual skin' and of menstrual discharge, respectively, could not be ascertained as yet (see also Christen, 1968, 1974). Up to now little research has been done on the physiological and hormonal aspect of reproduction in the Callithricidae (see for example Preslock, Hampton & Hampton, 1973). Hampton & Taylor (1971) emphasized the necessity to reconsider some problems of the reproductive physiology in marmosets such as the influence of a permanent corpus luteum in the female's ovaries and the extreme high levels of progesterone in marmosets (*Saguinus oedipus*, *Saguinus fuscicollis*).

In some catarrhine Primates (e.g. *Macaca Mulatta*, *Papio*) a close relationship exists between the physiological and the behavioural oestrus (see for example Altmann, 1962; Carpenter, 1942; Kaufmann, 1965; Loy, 1971; Michael, 1965; Michael, Herbert & Welegalla, 1966; Rowell, 1968; Zuckerman, 1932). The aim of this and following papers is to find out behavioural correlates to changes of the hormonal status in marmoset females in relation to oestrus, and, furthermore, whether behavioural elements or syndromes are adequate for determining more or less accurately the beginning and duration of oestrus.

2. Material and Methods

The allogrooming frequency of three pairs of adult *Callithrix jacchus* has been recorded before, during, and after 22 postpartum oestrus over a period of two to four years. Each pair lived with its offsprings in family groups (Gr. B, C, D). By the end of the study Gr. B had a membership of 18 (6♂♂, 12♀♀), Gr. C of 17 (10♂♂, 7♀♀), and Gr. D

of 8 (4♂♂, 4♀♀). The breeding pairs had the α -position of the social hierarchy. Gr. B and Gr. C lived in rooms (5.0 m $\times$ 4.0 m $\times$ 3.0 m and 4.0 m $\times$ 4.5 m $\times$ 2.5 m respectively), Gr. D in a wire cage (2.0 m $\times$ 2.0 m $\times$ 1.6 m). From the first to the 25th day following each parturition the three groups were observed daily; during the remaining period we took records on at least six days/week. The daily observation period lasted 51 min (3 $\times$ 15 min and 3 $\times$ 2 min). The statistical analysis was done with the χ^2 and the z -test.

3. Results

Allogrooming frequency during anoestrus

The three ♂♂ groomed more frequently than the three ♀♀ (Gr. B: $N = 1233$; $\delta = 64.89\%$; $X^2 = 54.62$; d.f. = 1; $P < 0.001$; Gr. C: $N = 1032$; $\delta = 62.69\%$; $X^2 = 33.26$; d.f. = 1; $P < 0.001$; Gr. D: $N = 764$; $\delta = 59.94\%$; $X^2 = 15.12$; d.f. = 1; $P < 0.001$). The mean allogrooming frequency for each pair and hour was 2.1 in Gr. B, 1.8 in Gr. C, and 1.4 in Gr. D. About one-quarter to one-tenth of the total grooming was initiated by an invitation gesture (see Epple, 1967; Fitzgerald, 1935; Rothe, 1971) by either ♂ or ♀ (Gr. B: (δ) $n = 241$; 30.12%; (η) $n = 118$; 27.25%; Gr. C: (δ) $n = 253$; 39.10%; (η) $n = 144$; 37.42%; Gr. D: (δ) $n = 113$; 24.67%; (η) $n = 97$; 31.67%). Only in Gr. D existed differences between the ♂ and the ♀ as to the frequency of grooming started by an invitation ($z = 2.13$; 3.6% $> P > 2.8\%$); that means that the ♂ initiated more grooming interactions by invitation than the ♀. The three ♂♂ refused fewer invitations for grooming than the ♀♀. The ♂♂ of Gr. B, C and D did not react to each 3.6, 3.0 and 3.7 invitation of the ♀♀, whereas the ♀♀ of Gr. B, C and D refused each 2.1, 1.9 and 2.9 invitation of the ♂♂. The mean duration of the grooming sessions was 17.1 sec (range: 5–327 sec) in Gr. B, 14.8 sec (range: 7–241 sec) in Gr. C, and 16.3 sec (range: 8–266 sec) in Gr. D. There were no significant differences between ♂♂ and ♀♀ as to the duration of active grooming. The ♂♂ of Gr. B and Gr. C ended just as many grooming interactions as the ♀♀. In Gr. D the ♀ withdrew from the ♂ significantly more frequently than vice versa ($X^2 = 5.54$; d.f. = 1; $P < 0.025$).

Allogrooming frequency from day 1 to day 4 postpartum

After 17 of 22 births, the level of allogrooming frequency did not differ from that before birth. After two births in Gr. B and Gr. C, and after one in Gr. D, the grooming activity increased to 3.7 interactions (Gr. B, to 3.3 (Gr. C), and to 3.8 (Gr. D)/hr. The number of grooming sessions initiated by invitation by either ♂ or ♀ did not differ significantly from that before birth in Gr. B and Gr. D, but decreased in Gr. C ($\delta = 29.85\%$; $\eta = 25.58\%$; $z = 2.11$; 3.6% $> P > 2.8\%$). In Gr. D the difference between ♂ and ♀ as to the frequency of grooming started by invitation was significant ($z = 2.15$; 3.6% $> P > 2.8\%$); that is, the ♂ invited the ♀ to grooming less often during the first four days postpartum than before birth. In Gr. B and Gr. C no such changes were to be seen, neither in the ♂♂ nor in the ♀♀. The ♂♂ refused each 3.5 invitation (Gr. B), each 3.0 (Gr. C), and each 2.0 (Gr. D), respectively; the ♀♀ did not react to each 2.0 (Gr. B), to each 2.0 (Gr. C) and to each 3.0 (Gr. D). The mean duration of the grooming sessions was not different to that before birth. Furthermore, the ♂♂ groomed as long as

the ♀♀. Beginning with the third day postpartum, the ♀♀ ended more grooming sessions than the ♂♂ (Gr. B: $X^2 = 6.72$; d.f. = 1; $P < 0.01$; Gr. C: $X^2 = 8.31$; d.f. = 1; $P < 0.01$; Gr. D: $X^2 = 12.63$; d.f. = 1; $P < 0.001$).

Allogrooming frequency from day 5 to day 11 postpartum

The allogrooming frequency increased enormously in comparison to that during the first four days postpartum (Gr. B: $X^2 = 156.31$; d.f. = 1; $P < 0.001$; Gr. C: $X^2 = 75.57$; d.f. = 1; $P < 0.001$; Gr. D: $X^2 = 11.53$; d.f. = 1; $P < 0.001$). The mean frequency/hr increased to 12.9 bouts in Gr. B, to 16.6 in Gr. C and to 6.0 in Gr. D. Significant differences existed between ♂♂ and ♀♀ (Gr. B: $N = 522$; $\delta = 87.54\%$; $X^2 = 150.21$; d.f. = 1; $P < 0.001$; Gr. C: $N = 890$; $\delta = 72.02\%$; $X^2 = 86.33$; d.f. = 1; $P < 0.001$; Gr. D: $N = 356$; $\delta = 70.51$; $X^2 = 15.33$; d.f. = 1; $P < 0.001$). After 17 of 22 births, we recorded the maximum of grooming frequency between the fifth and 11th day postpartum. Furthermore, the ♀'s willingness to copulate with the ♂ was the greatest one to three days following the absolute grooming maximum. The increase of the allogrooming activity was abrupt, that is, increasing suddenly from one day to the next in about 50%. The frequency of grooming sessions initiated by invitation decreased significantly (Gr. B: $\delta = 3.5\%$; $\eta = 10.76\%$; $z = 7.73$; $P < 0.3\%$; Gr. C: $\delta = 8.11\%$; $\eta = 11.64\%$; $z = 6.33$; $P < 0.3\%$; Gr. D: $\delta = 9.56\%$; $\eta = 8.57\%$; $z = 3.49$; $P < 0.3\%$). The differences between the ♂ and the ♀ as to the frequency of grooming initiated by invitation was significant only in Gr. B ($z = 2.66$; $0.9\% > P > 0.7\%$). The ♀♀ refused more grooming invitations than the ♂♂ and than before the 5th day postpartum (δ of Gr. B each 4.3, of Gr. C each 4.9, and of Gr. D each 2.1; η of Gr. B each 1.2, of Gr. C each 1.7, and of Gr. D each 2.1). The mean duration of the grooming sessions was 11.4 sec (range: 2–43 sec) in Gr. B, 14.1 sec (range: 1–57 sec) in Gr. C, and 13.9 sec (range: 7–38 sec) in Gr. D. In comparison to the anoestrus period the grooming duration was slightly shorter between day 5 and day 11 postpartum. The ♀♀ ended more groomings than the ♂♂ (Gr. B: $X^2 = 6.21$; d.f. = 1; $P < 0.025$; Gr. C: $X^2 = 5.88$; d.f. = 1; $P < 0.025$; Gr. D: $X^2 = 8.71$; d.f. = 1; $P < 0.01$).

Allogrooming frequency from day 12 to day 18 postpartum

In Gr. C and Gr. D the allogrooming frequency decreased in relation to the foregoing week (Gr. C: $N = 478$; $\delta = 54.81\%$; $X^2 = 62.04$; d.f. = 1; $P < 0.001$; Gr. D: $N = 206$; $\delta = 69.41\%$; $X^2 = 20.01$; d.f. = 1; $P < 0.001$). No such changes in allogrooming activity were to be seen in Gr. B ($N = 459$; $\delta = 65.57\%$; $X^2 = 2.02$; d.f. = 1; $P > 5.0$). The mean allogrooming frequency for each pair and hour was 11.3 in Gr. B, 8.9 in Gr. C and 3.5 in Gr. D. Significant differences in grooming frequency existed between ♂ and ♀ in Gr. B and Gr. D ($X^2 = 22.28$; d.f. = 1; $P < 0.001$ and $X^2 = 15.54$; d.f. = 1; $P < 0.001$). In Gr. C no such differences could be ascertained ($X^2 = 2.21$; d.f. = 1; $P > 5.0$). No conception took place after the 11th day postpartum, but after five births (2 in Gr. B and Gr. C, one in Gr. D) we recorded the absolute allogrooming maximum after the 11th day postpartum. By the 18th day at the latest the allogrooming activity reached that recorded before birth, with the exception of four postpartum periods. As a rule the grooming decreased continuously beginning with day 12 postpartum. The decrease was abrupt, that is from one day to the following only

after four births. Sexual willingness of the ♀ was evidenced only one time (Gr. B) after the 11th day postpartum. Allogrooming initiated by invitation increased in Gr. B and Gr. D (Gr. B: ♂ = 11.29%; ♀ = 7.59%; $z = 2.30$; $P = 2.1\%$; Gr. D: ♂ = 14.68%; ♀ = 20.63%; $z = 2.54$; $1.2\% > P > 0.9\%$). No changes in actively initiated grooming occurred in Gr. C (♂ = 8.77%; ♀ = 4.16%; $z = 1.84$; $7.2\% > P > 5.7\%$). In Gr. C and Gr. D the number of groomings, initiated by the ♀ in relation to the total grooming frequency of the ♂ remained constant (Gr. C: $z = 0.32$; $76.3\% > P > 68.9\%$; Gr. D: $z = 1.83$; $7.22\% > P > 5.7\%$), whereas in the ♂ of Gr. B, the frequency of positive reactions to the ♀'s invitations increased ($z = 4.20$; $P < 0.3\%$). The reaction to grooming invitations by the ♂♂ remained constant in Gr. B ($z = 0.77$; $48.0\% > P > 43.4\%$), decreased in Gr. C ($z = 2.96$; $0.4\% > P > 0.3\%$), and increased in Gr. D ($z = 2.05$; $P = 3.6\%$). The ♂ of Gr. B refused each 3.8 invitation, the ♀ of Gr. B each 1.4; the corresponding data for Gr. C were 4.1 (♂) and 1.7 (♀). The ♂ of Gr. D did not react on each 2.0 invitation and the ♀ refused each 1.8. The mean duration of the grooming sessions was 15.2 sec (range: 4–57 sec) in Gr. B, 12.8 sec (range: 3–39 sec) in Gr. C and 9.4 sec (range: 3–24 sec) in Gr. D. No significant differences as to the duration of grooming sessions existed between ♂♂ and ♀♀. The ♀♀ ended more groomings than the ♂♂ (Gr. B: $X^2 = 5.82$; d.f. = 1; $P < 0.025$; Gr. C: $X^2 = 6.71$; d.f. = 1; $P < 0.01$; Gr. D: $X^2 = 8.90$; d.f. = 1; $P < 0.01$).

Allogrooming frequency from day 19 to day 25 postpartum

The allogrooming frequency reached the level observed in anoestrus, i.e. before birth. No significant differences in grooming activity existed between the ♂ and the ♀ of each group (Gr. B: $N = 89$; ♂ = 64.04%; $X^2 = 3.51$; d.f. = 1; $P > 5.0$; Gr. C: $N = 114$; ♂ = 55.26%; $X^2 = 0.63$; d.f. = 1; $P > 5.0$; Gr. D: $N = 61$; ♂ = 52.46%; $X^2 = 0.07$; d.f. = 1; $P > 5.0$). The mean allogrooming frequency/hr was 2.2 in Gr. B, 2.1 in Gr. C and 1.0 in Gr. D. The amount of grooming initiated by invitation was lower in Gr. B and Gr. C and higher in Gr. D (Gr. B: ♂ = 22.80%; ♀ = 28.12%; Gr. C: ♂ = 28.85%; ♀ = 22.34%; Gr. D: 43.75%; ♀ = 31.03%). Between ♂ and ♀ no differences could be ascertained as to the initiated grooming (Gr. B: $z = 0.56$; $61.7\% > P > 54.8\%$; Gr. C: $z = 0.79$; $48.4\% > P > 42.4\%$; Gr. D: $z = 1.76$; $8.9\% > P > 7.2\%$). In comparison to the period from day 5 to day 11 postpartum, the level of allogrooming initiated by either ♂ or ♀ decreased with the exception of the ♀ of Gr. D (Gr. B: (♂) $z = 2.36$; $2.1\% > P > 1.6\%$; (♀) $z = 2.84$; $0.5\% > P > 0.4\%$; Gr. C: (♂) $z = 4.38$; $P < 0.3\%$; (♀) $z = 4.33$; $P < 0.3\%$; Gr. D: (♂) $z = 3.71$; $P < 0.3\%$; (♀) $z = 1.08$; $31.7\% > P > 27.1\%$). The mean duration of the grooming sessions was 15.3 sec (range: 6–59 sec) in Gr. B, 16.9 sec (range: 3–82 sec) in Gr. C and 10.1 sec (range: 4–67 sec) in Gr. D. No differences existed between ♂♂ and ♀♀ in this respect. The ♂♂ of Gr. C and Gr. D ended as many grooming sessions as the ♀♀, whereas the ♀ of Gr. D withdrew from the ♂ more frequent than vice versa ($X^2 = 5.67$; d.f. = 1; $P < 0.025$).

Allogrooming frequency of α -♂ and α -♀ in relation to group size

In all three groups we observed the trend for more grooming by the α -♂ and the α -♀ with increasing group size, that is with increasing number of adult and sexually mature sons and daughters.

4. Discussion

The results clearly show that allogrooming is an essential component of behavioural oestrus in *Callithrix jacchus* (see also Rothe, in press; Altmann, 1962; Carpenter, 1942; Hall, 1962; Kaufmann, 1965; Loy, 1971; Michael, 1965 for *Catarrhina*). However, up to this time it is impossible to determine exactly the beginning and the duration of postpartum oestrus by analysing grooming activity (see for example Michael & Herbert, 1963; Rowell, 1968). In consideration of all results we have obtained from the analysis of grooming and copulatory behaviour (Rothe, in press) we conclude that the postpartum oestrus in *C. jacchus* ♀ ♀ lasts at least an average of 9 to 11 days. The sexual willingness of the ♀, however, is restricted to 5 to 6 days with a slight peak at 2 to 3 days. Our results indicate that the sexual willingness of the ♀, and most often the maximum of allogrooming frequency culminates between the 5th and the 11th day postpartum. The maximum of allogrooming activity frequently precedes the maximum of copulatory behaviour and sexual willingness of the ♀. Since copulations with intromission and ejaculation seldom occur before maximal sexual willingness of the ♀ we tentatively assume that the day of conception does not coincide with the day of greatest grooming activity.

Preslock, Hampton & Hampton (1973) found a cyclic variation of plasma progesterone and estrogen levels in *Saguinus oedipus* and *Saguinus fuscicollis*. In consideration of this variation the authors assume a reproductive cycle of 15.5 ± 1.5 days (based on the interval of two progesterone peaks). The reproductive cycle length of *S. oedipus* and *S. fuscicollis* seems to contrast to some extent with our data on the duration of postpartum oestrus in *C. jacchus* based on analysis of behaviour (see also Rothe, in press). But if we consider that the level of grooming activity drops gradually within a period of 4 to 6 days and that slight changes of the hormonal status do not have always detectable behavioural correlates, we find rather good conformity of the physiological and behavioural data, keeping in mind that differences between species may exist.

The role of pheromones in the behaviour of Callithricidae and some catarrhine primates has been emphasized (Epple, 1972; Michael & Keverne, 1968, 1970). We do not know, however, whether the ♂'s behaviour, i.e. the increased grooming activity is directly stimulated by increased release of pheromone of vaginal origin and/or hormones by the ♀ or whether the change of the ♀'s behaviour is responsible to its (♀) attractiveness for the ♂. Probably both—pheromones/hormones and the ♀'s behaviour influence and stimulate the ♂'s interaction activity.

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Ronald D. Nadler

*Yerkes Regional Primate Research
Center,
Emory University,
Atlanta, Georgia, U.S.A.*

John T. Braggio

*Department of Psychology,
Georgia State University,
Atlanta, Georgia, U.S.A.*

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Sex and Species Differences in Captive-reared Juvenile Chimpanzees and Orang-utans

The behavior of nursery-reared juvenile chimpanzees and orang-utans was studied during intraspecific group interactions in large outdoor compounds. Chimpanzees spent more time on the ground, more time in proximity to another and exhibited more slap-hit behavior than the orang-utans. Both groups exhibited only species-typical vocalizations. Males of both species were more assertive in social interactions, whereas females interacted more with inanimate objects. Positive correlations between body weight and the frequency of some social interactions partially confounded interpretation of the sex differences. The results indicate that early experience with adults is not necessary for the development of certain sexually dimorphic and species-typical behavior patterns in juvenile apes. However, early experience with peers seems to facilitate development of these patterns. The results are discussed in relation to available data on the early hormonal and social determinants of behavior in the higher Primates.

1. Introduction

Our ability to evaluate the comparative implications for Man of data obtained on any one of the *Pongidae* is enhanced by evidence of both the similarities and differences between the individual species. Such evidence enables us to broaden our evolutionary perspective of Primate behavior generally and especially, to appreciate better the relationship between Man and his taxonomic affiliates. Field studies of chimpanzees (Kortlandt, 1962; Goodall, 1965; Reynolds & Reynolds, 1965) and orang-utans (Davenport, 1967; MacKinnon, 1971; Horr, 1972) indicated that significant differences did, in fact, exist between these two species in basic aspects of their life styles. Chimpanzees were found to be gregarious animals living together in complex social groups of 60–80 animals. These large groups were not stable, however, and were generally fragmented into smaller sub-groups of 2–30 animals, consisting of animals of both sexes and all age categories. These studies showed that chimpanzees were both arboreal and terrestrial, traveling primarily on the ground during their daily nomadic excursions, but spending 50–75 % of each day eating or resting in trees. Orang-utans, on the other hand, were found to be semi-solitary, essentially asocial animals with an average group size of less than two. The modal group size of two individuals reflected the preponderance of mother-infant sightings, but solitary individuals were frequently observed as well. Orang-utans were observed primarily in the lower jungle canopy, 20–60 ft above the ground, although they did descend on occasion to eat, drink and to escape observation.

In light of the differences observed between chimpanzees and orang-utans in the field, it was of interest to study the behavior of captive-reared animals that never experienced the conditions of their natural habitat nor ever interacted with adult conspecifics. Such animals, raised from birth under similar conditions in the laboratory, obviously could not learn species-typical behavior from experienced wild-born adults. This profound deficiency in early experience, one of the major contributors to behavioral organization of animals generally (Schneirla, 1966), should be especially significant for the phylogenetically advanced *Pongidae*, in comparison to the lower animal species, because of their greater

dependence on learning (Mason, 1965). Therefore, the patterns of social interaction and the behavioral adaptations to the environment acquired by such animals, in some sense reflect more directly on the biological heritage of the species than would the behavior of animals reared under natural conditions, since the behavior of the latter animals would be confounded by experience with adults.

2. Method

Subjects

The composition of the two groups of chimpanzees and orang-utans used in the present study is shown in Table 1. As can be seen, the chimpanzee group consisted of eight animals, the orang-utan group five, with two females in each group. In addition, whereas both of the females in the chimpanzee group weighed less than any one of the males, one of the female orang-utans, Guchi, was older and weighed considerably more than the heaviest male orang-utan.

Table 1 **Group composition for chimpanzees and orang-utans used in the present study**

Name	Sex	Age (months)	Weight (kg)
Chimpanzees (<i>Pan troglodytes</i>)			
Robert	M	29	8.92
Richard	M	31	9.82
Charles	M	33	10.51
Sanford	M	39	10.32
Ubar	M	44	16.58
Hook	M	46	12.94
Francisca	F	30	8.70
Heppie	F	38	8.70
Orang-utans (<i>Pongo pygmaeus</i>)			
Loklok	M	39	15.56
Bebas	M	40	17.28
Kanting	M	44	15.24
Tiga	F	47	10.64
Guchi	F	56	23.36

History of the subjects

All except one of the animals used in the present study were born at the Yerkes Regional Primate Research Center, separated from their mothers at birth and reared in the nursery by human caretakers. The animals were placed individually in incubators shortly after birth and remained there until they were 3-5 months of age. They were then removed and caged in pairs, one male with one female, whenever possible. Cage mates were changed routinely every few months except during the experiment, for which the same animals remained together throughout.

The one exception to the above schedule was the male orang-utan, Bebas, who was obtained from the Fort Worth Zoo when he was three and one-half months of age, having been separated from his mother at birth. In contrast to the other animals which were socialized before they were one year of age, Bebas lived alone in a cage until he was

almost two years old. However, since he lived in the same room with the other orang-utans, he had the opportunity to observe them prior to the time he was given physical access to them.

Apparatus

Two enclosed compounds of different size were used in the present study. The large compound was 27.7 m $\times$ 40.1 m, while the small compound was 14.8 m $\times$ 36.0 m. Around the periphery of each compound there was a wire mesh fence that was designed to prevent the subjects from escaping from the observation area. Inside each of the two compounds there was a three dimensional structure of horizontal and vertical bars and a large wooden table. The items in each compound were identical in size. On the ground of each of the compounds there were patches of soil, grass, weeds and an assortment of small stones.

Procedure

For the duration of the experiment the orang-utans and chimpanzees were observed as two separate groups during the months of July, August and September 1972. The daily test sessions started at approximately 1.00 p.m. The subjects were observed five days each week, Monday through Friday, weather permitting. The experiment was terminated after 35 observation sessions were obtained for each animal in each of the two groups. During the daily test sessions the observations that were made on the various subjects were recorded in the form of frequency and duration of different behavioral categories.

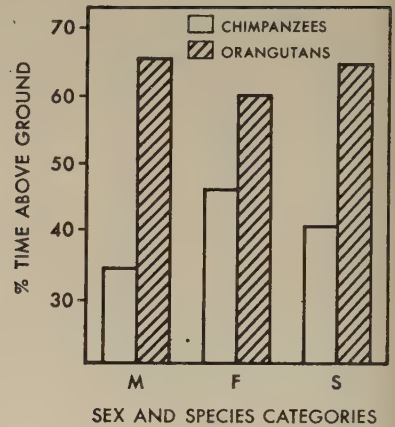
The daily observation procedure consisted of taking the orang-utans outside first and putting them inside the small enclosed compound. Once the animals were in the compound, five minutes were allowed to elapse before the start of the first observation period, in order to permit them to habituate to each other and to the stimulation of being handled by the human caretakers. Each of the animals was observed by the Experimenter at a distance of 2-3 m. from the fence for 10 consecutive 30 sec. periods. In order to control for intrasession habituation effects, the order of the daily observations was randomly varied for each of the five animals. After each orang-utan was observed once for a total of 300 sec, the group was returned to the nursery and the chimpanzees were taken outside and placed inside the large compound. Following the 5 min. habituation period, the eight chimpanzees were observed according to the same schedule described for the orang-utans.

3. Results

Data analysis

Statistical analyses were performed on the data to determine the probabilities of occurrence of the different observed events. Since the level of measurement consisted of ordinal values, all statistical analyses were performed by using nonparametric tests. The Mann-Whitney *U* test was used to make comparisons between two independent samples, the Wilcoxon matched-pairs signed-ranks test (*T*) was used to make comparisons between two related samples, and the Spearman rank-order correlation coefficient was used to compute the degree of association present between two variables (Siegel, 1956). In

Figure 1. Percentage of total time juvenile chimpanzees and orangutans spent above the ground. M = males, F = females, S = species; males and females combined.



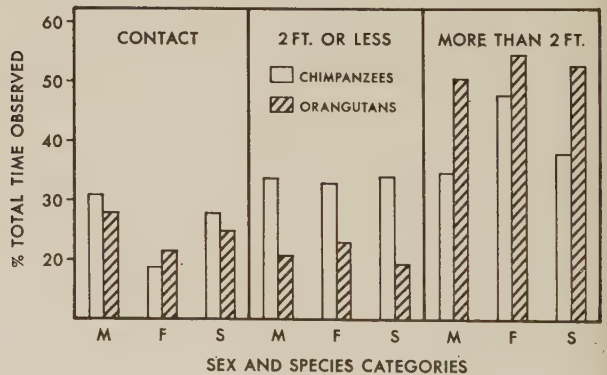
some cases, the number of observations available for a given group on a particular category was unusually small so that the probability of occurrence of the observed event could not be computed beyond the 0.05 level of significance.

Use of environment

Percentage of total time spent above the ground. Figure 1 illustrates that the orang-utans spent significantly more time above the ground than the chimpanzees ($U = 0$, $P < 0.01$). That is, the chimpanzees spent only 40% of their time above the ground whereas the orang-utan spent 64% of their time above the ground. The results of a second statistical analysis indicated that there were no significant sex differences in either species with respect to this measure ($U = 14$, $P > 0.05$).

Type and duration of intra-animal spacing. Figure 2 shows that the type and duration of spacing between animals differed as a function of the species and sex variables. The

Figure 2. Percentage of total time juvenile chimpanzees and orangutans spent in contact with another animal (panel 1), not in contact but within two ft of another animal (panel 2) and more than two ft from another animal. M, F and S have same meaning as in Figure 1.



first panel of Figure 2 shows that chimpanzees did not differ significantly from orang-utans with respect to the total amount of time spent in direct body contact with another animal (male or female) ($U = 14$, $P > 0.05$). However, males of both species spent a greater percentage of their total time in direct body contact with another animal than did the females ($U = 3$, $P < 0.05$). The second panel of Figure 2 shows that chimpanzees spent a greater percentage of their total time in proximity to another animal at distances of 2 ft or less than did the orang-utans ($U = 0$, $P < 0.01$), and there were no significant sex differences for either species with respect to that measure ($U = 0$, $P > 0.05$). Finally, the third panel of Figure 2 indicates that orang-utans spent a greater percentage of the total time at distances that were greater than 2 ft from another animal than did the chimpanzees ($U = 6$, $P < 0.05$), and that outcome was not accompanied by a significant sex difference either ($U = 7$, $P > 0.05$).

Activity profiles

Table 2 shows the activity profiles for chimpanzees and orang-utans of both sexes. The summary table was derived by converting the absolute frequencies for each behavioral category into relative frequencies. For the most part, the categories of behavior which are discussed in detail in this section are those for which statistically significant differences were found between species or sexes.

Approach-retreat. Statistical analyses performed on these data indicated that none of the overall comparisons were significantly different. However, more detailed analyses of the average frequencies of approach and retreat revealed the presence of interactions that were related to the sex variable. There were no significant differences in differential approach or retreat according to sex for the females of either species. However, male chimpanzees initiated approaches towards other males more frequently than towards

Table 2 **Activity profiles for juvenile chimpanzees and orang-utans**

Behavioral category	Chimpanzees			Orang-utans		
	Male <i>N</i> = 6	Female <i>N</i> = 2	Group <i>N</i> = 8	Male <i>N</i> = 3	Female <i>N</i> = 2	Group <i>N</i> = 5
Approach	0.13	0.11	0.12	0.14	0.09	0.12
Retreat	0.11	0.14	0.12	0.11	0.11	0.11
Rough and tumble	0.11	0.05	0.09	0.12	0.08	0.11
Play face	0.09	0.06	0.09	0.10	0.07	0.09
Chase	0.05	0.03	0.04	0.03	0.02	0.03
Slap-hit	0.04	0.06	0.05	0.02	0.01	0.02
Game	0.01	0.01	0.01	—	—	—
Embrace	0.02	0.02	0.02	0.01	0.01	0.01
Social examination	0.01	—	0.01	—	—	—
Genital examination	0.02	0.02	0.02	0.02	0.02	0.02
Groom	0.06	0.07	0.07	0.04	0.06	0.05
Object examination	0.12	0.16	0.13	0.14	0.20	0.16
Oral examination	0.12	0.18	0.13	0.13	0.21	0.16
Eat	0.03	0.04	0.03	0.04	0.03	0.03
Stereotype	0.02	0.01	0.02	0.04	0.03	0.04
Erection	0.01	—	0.01	—	—	—
Masturbate	—	—	—	—	—	—
Mount	0.01	0.01	0.01	—	—	—
Present	0.01	0.01	0.01	—	—	—
Vocalizations	0.03	0.03	0.03	0.05	0.07	0.06

females ($T = 0$, $P < 0.05$, one tail) and also retreated more frequently from other males than from females ($T = 0$, $P < 0.05$). In contrast to this pattern for the male chimpanzees, no significant differences were obtained with respect to these data for the orang-utans. This outcome appears to be due to the more heterogeneous composition of the orang-utan group in terms of the animals' body weight. It was noted above that the female, Guchi, was the heaviest animal in the group of orang-utans. Analysis of the individual data for the five orang-utans revealed that Guchi was the animal that was approached most often by each of the three males. As such, Guchi appeared to function as another male with respect to those data. Guchi also retreated less frequently from the males than did Tiga, the other female orang-utan. The hypothesis that the frequency of retreats from an animal was related to its body weight was supported by the significant positive Spearman rank-order correlation coefficient between those two variables for both species ($r = 0.90$, $P < 0.05$).

Rough and tumble interactions. Interestingly, several other behaviors shown in Table 2 differentiated males of both species from females. The males of both species showed a greater proportion of rough and tumble behaviour than the females ($U = 6$, $P < 0.05$, one tail). On the other hand, females of both species showed a higher proportion of object examination ($U = 0$, $P < 0.01$), and a higher proportion of oral examination ($U = 0$, $P < 0.01$) than the males. Additional analyses of the data on rough and tumble behavior indicated that the male-male interactions were significantly more frequent than female-female interactions for each species ($U = 0$, $P < 0.036$, one tail). Moreover, for the chimpanzees the frequency of the male-female interactions was greater than the female-female, but less than the male-male. For the most part, the orang-utans showed the same type of relationship with respect to that measure, i.e. male predominance in rough and tumble behavior. However, for the orang-utans, the male-female interactions were the most frequent of the three types of interactions. The elevated frequency of the male-female interactions in the orang-utans seemed to reflect the high frequency with which the males approached the female Guchi. That interpretation is partly supported by the positive correlation between body weight and the frequency of rough and tumble behavior which approached significance ($r = 0.60$, $0.05 < P < 0.10$).

Facial expressions and rough and tumble interactions. Examination of these data showed that there was a direct relationship between the "play-face" (Van Hooft, 1962) and rough and tumble interactions. Both measures were higher in males than in females ($U = 4$, $P < 0.05$). Further, in many circumstances the appearance of the play-face preceded the occurrence of these peer interactions. When that relationship was explored by determining the Spearman rank-order correlation coefficient, it was found that there was a significant correlation between the rank order of rough and tumble interactions and the rank order of the play-face expression in chimpanzees ($r = 0.86$, $P < 0.01$) and in orang-utans ($r = 0.90$, $P < 0.05$).

Additional categories which exhibited significant species differences were those of slap-hit behavior and vocalizations. Chimpanzees engaged in a greater proportion of slap-hit behavior than the orang-utans ($U = 0$, $P < 0.01$). Regarding the vocalization category, screams and hoots occurred only in chimpanzees, whereas whimpers occurred only in orang-utans. Since there was no overlap between the two species with respect to the type of vocalizations emitted, the data indicate that this behavior was clearly species-typical.

As can be seen in Table 2, stereotypies occurred relatively infrequently during the formal tests of the subjects in this study. The most common form of stereotypy in the

chimpanzees consisted of rocking while sitting. Repetitive swinging against the fence while suspended therefrom was the most common form in the orang-utans, most of whom exhibited this behavior very infrequently. The one orang-utan on which relatively frequent observations of stereotyped behavior were recorded was Bebas, the animal that lived alone for the longest period of time. In this case, the stereotypy consisted of the animal leaping forward from a sitting position or from a position on the fence, while clutching its own body with both arms, resulting in the animal landing on its chest and chin. Additional observations, though unsubstantiated by systematic data, gave the impression that both species of apes exhibited stereotypes more frequently when they were in their home cages than when they were in the outdoor compounds.

4. Discussion

The results indicate that chimpanzees and orang-utans, in spite of being raised from birth under similar conditions in the laboratory, exhibited a number of species differences in their interactions with the environment and in their social relations with peers. The juvenile orang-utans spent 50% more time on structures above the ground than did the chimpanzees, a relationship that was strikingly similar to comparable behavior reported for orang-utans (Davenport, 1967; MacKinnon, 1971; Horr, 1972) and chimpanzees (Kortlandt, 1962; Goodall, 1965; Reynolds & Reynolds, 1965) in the field. This difference in behavior is associated with obvious anatomical differences between the species (Schultz, 1940, 1941), as apparently are the species-typical vocalizations exhibited by these animals (Negus, 1949). As such, it seems likely that these anatomical differences exerted a major influence on development of the different accommodations to the environment observed in the two species. The greater incidence of slap-hit behavior in chimpanzees as compared to orang-utans may reflect an indirect influence of morphological factors in that the chimpanzees, which spent more time on the ground, had their hands available for greater involvement in such activity than did the more arboreal orang-utans.

More provocative than the behavioral differences described above was the difference in intra-animal spacing observed in the juvenile apes, since that measure is not readily relatable to structural differences between the species. The laboratory-reared apes exhibited patterns of sociability that appeared to reflect the patterns of their respective wild-born counterparts, in that the chimpanzees maintained closer proximity to peers than did the orang-utans. It is difficult to speculate on the significance of this finding or on the relationship between intra-animal spacing in the laboratory and social organization in the field. However, we anticipate that additional research on these species, conducted earlier in development, will help to uncover behavioral precursors of the species-typical patterns reported in this study that will aid in their further interpretation.

In addition to the species differences discussed above, there was also observed a number of sex differences in the behavior of both species. The data on body contact, approach and retreat behavior and rough and tumble interactions all seem to reflect a common propensity of the males to initiate social interactions more frequently than the females and to participate in these activities for longer periods of time than the females. The females, for their part, interacted with inanimate objects more frequently than the males.

Our finding in both chimpanzees and orang-utans that male-male interactions

predominated over female-female interactions with respect to rough and tumble behavior corresponds to a similar finding in juvenile gorillas (Freeman & Alcock, 1973). These data on young apes suggest that males are more assertive than females in social interactions and agree with earlier results on similar behavior in young rhesus monkeys (Rosenblum, 1961) and children (Maccoby, 1966). Considered together, the data suggest that a pervasive trend exists among the higher Primates for the appearance of sexual dimorphism in social behavior well before sexual maturity.

In recent years, numerous studies have investigated the ontogeny of sexually dimorphic behavior in lower laboratory animals (Whalen, 1971). The results suggest that differentiation of sexual behavior is significantly influenced by exposure to male hormone during fetal and neonatal stages of development. Experimental studies on the rhesus monkey (Goy & Resko, 1972) and "experiments of nature" in humans (Money & Ehrhardt, 1972) suggest that male hormone exerts a comparable inductive influence on sexual differentiation of these higher Primates and, with respect to non-sexual behavior as well. Of course, behavioral development of animals higher on the evolutionary scale is influenced to a greater degree by social and cultural factors. The latter two presumably interact with hormonal influences to determine the ultimate expression of sexual dimorphisms (Diamond, 1965).

The importance of early social interactions for behavioral development in Primates was demonstrated most convincingly in studies of animals deprived of such early experience. Rhesus monkeys (Mason, 1960) and chimpanzees (Rogers & Davenport, 1969; Riesen, 1971) reared in social isolation not only failed to develop appropriate sexual orientation, but demonstrated little proficiency, if any, in general social behavior. Moreover, the behavior of those animals was dominated by the performance of various stereotypies.

The animals in the present study displayed stereotyped behavior infrequently when observed in the outdoor compounds, but apparently more frequently in their home cages. Whether or not the infrequent occurrence of stereotypies in the compounds was related to the environmental conditions in which they were observed (Berkson, Mason & Saxon, 1963) or to the earlier age at which the animals were socialized, compared to the chimpanzees of the earlier studies, cannot be determined conclusively at this time. The observations of frequent and varied social interactions between our animals suggest that their more moderate early deprivation produced less behavioral debilitation than the longer periods of isolation previously employed. This suggestion gains additional support from the fact that the highest frequency of stereotyping occurred in the animal that lived in physical isolation from peers for the longest period of time.

Our study of juvenile chimpanzees and orang-utans provides some tentative conclusions regarding behavioral development in these higher Primates. It is clear that neither early experience with, nor tutoring by adult conspecifics was necessary for development of the various examples of species-typical and sexually dimorphic behavior observed in our subjects. On the other hand, it is probable that early socialization with peers during the first year of life did contribute to the results obtained. Some of the species differences reported, such as those related to the animals' interaction with the environment, most likely derive from anatomical specializations of adaptive value acquired through evolution. The species differences in intra-animal spacing appear to be related to species-typical patterns of social organization in these animals. However, the mechanism by which these patterns are transmitted from generation to generation requires elucidation. The

examples of sexually dimorphic behavior recorded in the young apes represent a phenomenon that is common to the higher Primates, including Man, i.e. a propensity of males for greater social assertiveness and interaction than females. Hormonal influences have been implicated in the development of sex differences in a number of species, but no information on this question is available for the apes. Since body weight was related to some of the sex differences observed, that factor may represent one avenue by which these differences are established in young animals of comparable age. However, it is unlikely that such a mechanism would account completely for development of sexually dimorphic behavior under natural conditions. The comparability between some of the data obtained on these apes and other data reported for monkeys and humans encourages us to continue exploring these broad issues in behavioral development in order to define more adequately trends within the order *Primates* which have relevance for concepts pertaining to human evolution.

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Christopher L. Coe

Sexual Segregation and its Ontogeny in Squirrel Monkey Social Structure

Leonard A.
Rosenblum

*Primate Behavior Laboratory,
State University of New York,
Downstate Medical Center,
Brooklyn, New York, U.S.A.*

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Four groups of squirrel monkeys were observed to determine the primary basis of adult group structure. These studies included observations on (1) intact and gonadectomized males and females during and after breeding; (2) intact adults only; (3) subadults only; and, (4) a mixed group of adults and subadults. The spatial distribution of subjects in each group was used as a basic measure of social organization. It was found that for adults, regardless of hormonal status, between-sex distances were consistently greater than within-sex distances. This sexually segregated adult structure was largely attributable to the females' attraction to one another and overt rejection of the males. Subadults by themselves did not show any clear sexual segregation. However, in the presence of an adult structure, the subadults gradually manifested the segregated pattern of the adults by gravitating toward same-sex adults. These results indicate that the socialization process, rather than endogenous hormonal status, is the major determinant of adult social structure in squirrel monkeys.

The structure and organizing principles of living and ancestral Primate groups have been the subject of much speculation. Some authors have suggested that the reproductive pair is a basic social form from which more elaborate group composition developed (Crook & Gartlan, 1966). However, the appearance of truly monogamous groups in Primates is limited only to several specialized members, i.e. Indriidae, Callithricidae, *Callicebus* and *Hylobates*. As a model for the ancestral Primate stage it may be more appropriate to consider the prosimian social pattern, since the prosimians closely resemble the morphological adaptations of the Paleocene Primates. One of the most prominent prosimian patterns (Martin, 1972) involves spatially organized aggregations as opposed to integrated groups. In this arrangement, females are more aggregative than males, sharing a central core of home ranges around which relatively solitary males array themselves.

It is reasonable to suggest that cohesive troops with a social structure involving sustained male and female membership could have evolved from this type of social pattern. The more integrated structure is characteristic of simian Primates and its emergence may have coincided with evolutionary elaborations of the brain and concomitant increases in communicative and learning abilities. Squirrel monkeys (*Saimiri sciureus*) may be particularly good models of the early simian pattern because this species manifests many of the presumed characteristics of the early simians. They are small in size, diurnal, extremely aboreal, insectivorous, and strictly seasonal breeders with a short estrous cycle. In addition, they utilize scent-marking and olfactory communication, are of comparatively low intelligence and engage in relatively delimited social interaction (Davis *et al.*, 1968, Rosenblum & Cooper, 1968).

The organization of squirrel monkey troops has been classified as intermediate grade in complexity, i.e. they associate in age-graded, multi-male aggregations in which the males are spatially separate from the more numerous females (Crook & Gartlan, 1966; Eisenberg, Muckenhirn & Rudran, 1971). Field data on *Saimiri* suggest that the troops are cohesive but with males hierarchically organized and traveling separately at the periphery of the female group (Baldwin, 1968, 1971). Social interaction between sexes

is infrequent and often agonistic. This homosexual cohesiveness has also been demonstrated in laboratory experiments (Mason & Epple, 1968; Candland *et al.*, 1973).

The field data indicate also that the females are the social unifiers and leaders of the troop (Baldwin, 1968). A further indication of the nature of female sociability, is the fact that female admittance to a new laboratory group is relatively rapid and hostile behavior to the newcomer is minimal (Rosenblum, Levy & Kaufman, 1968). However, in inter-group encounters females react more actively than males in the aggressive behavior of the winning group (Castell, 1969). This capacity of females to manifest dominance-related behavior is especially interesting since female *Saimiri* do not normally show evidence of a dominance hierarchy (Baldwin, 1968; Castell & Heinrich, 1971) except under selected conditions of stress (Talmage-Riggs & Anschel, 1973).

The purpose of this paper is to delineate further the structural dynamics of squirrel monkey groups. The current studies attempt to determine the quantitative dimensions of the counterposed forces of aggregation and dispersion of male and female squirrel monkeys under controlled laboratory conditions. In addition, the studies assessed several of the behavioral, hormonal, and developmental factors which underlie the characteristic adult pattern of a sexually segregated group structure.

1. Subjects

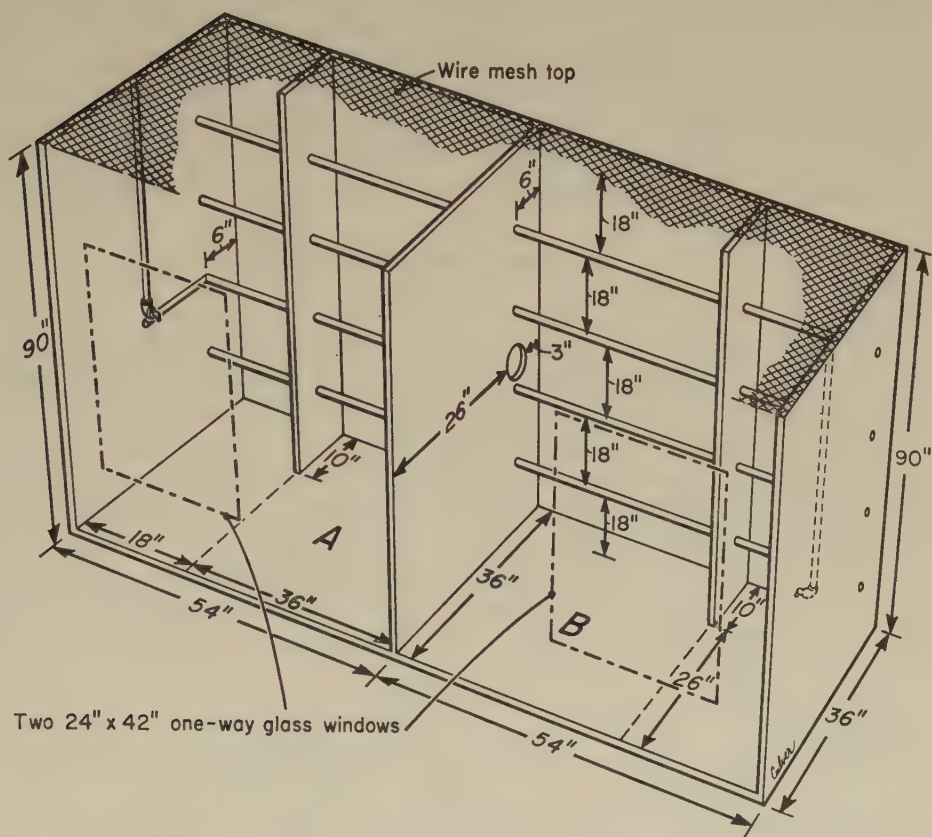
Fifty squirrel monkeys (*Saimiri sciureus*) were established in four study groups (see Table 1). All adults were wild-born, of the Peruvian variety, well acclimated to the laboratory,

Table 1 Designation of study groups and subject characteristics

Study	Designation	Subjects	N	Group size	Weight (g)/ origin	Observation length
I	Breeding (2 matched groups)	(a) Adult Females	16 (8 + 8)	15	641/wild	3 weeks
		(b) Adult Males	6 (3 + 3)		851/wild	(group formation)
		(c) Ov - x Females	4 (2 + 2)		536/wild	3 weeks
		(d) Castrate Males	4 (2 + 2)		737/wild	(4 months later)
II	Single-age: adults	(a) Adult Females	5	10	608/wild	3 weeks
		(b) Adult Males	5		835/wild	(group formation)
III	Single-age: subadults	(a) Subadult Females	5	10	654/lab.	4 weeks
		(b) Subadult Males	5		680/lab.	(group formation)
						1 week (after study IV)
IV	Mixed-age: adults + subadults	Subjects of Studies II + III		20		3 weeks (after Study III)

and chosen for similar weights and unfamiliarity with other members of the same sex. The gonadectomized animals used in Study I had been operated on post-pubertally more than three years prior to the present study. The subadults were laboratory-reared by wild-born mothers living in social groups and were 33–39 months of age when testing began. These younger subjects were considered subadults based on prior developmental data from our laboratory which indicated puberty for females at about three years and males about one year later (Rosenblum, 1972). Most subadults were familiar with one another although not with the adult subjects prior to this experiment.

Figure 1. Diagrams of the living areas employed in all studies. All figures are in inches. Note identical construction of the adjoining pens and the 7 in connecting tunnel.



2. Apparatus-housing

All groups were studied in living areas (see Figure 1) which consisted of two pens connected by a 18 cm diameter tunnel. The perch structure in each pen was identical and consisted of four aluminum pipe shelves evenly spaced from the tile floor to the mesh ceiling. In addition, each shelf was divided by a vertical partition one-third of the distance from the outer wall. This arrangement allowed the pen to be divided into 26 cm square cells for recordings of animal locations and computation of interanimal distances. Each front door contained a 0.75×1.2 m one-way observation mirror through which all observations were made. Feeding occurred once each afternoon and water was available *ad libitum* by means of two automatic watering spouts in each pen. The illumination schedule was constant for all studies—12 hr light, 12 hr dark.

3. Procedure

The four phases of the project were run successively over a nine month period beginning in May 1973. The groups in Study I were established and observed for three weeks

following formation and again four months later. These Study I groups were maintained for future research which will be reported separately. The subjects of Study II were placed together and observed for three consecutive weeks. Following these observations, this adult group was removed and housed in another pen while the subadults of Study III were observed for four weeks. At the conclusion of Study III, the influence of an adult structure on the behavior of these subadults was assessed by merging the adults of Study II with this group. These 20 *Ss* were studied for three weeks after which the adult group was removed and the subadults observed for one additional week to determine whether any residual effects of living with adults could be observed.

4. Observations

Study I

The simultaneous location of all subjects within each pen of the living area was recorded on schematic pen diagrams. During Study I four of these diagrams were completed each observation day (two A.M. and two P.M.), three days per week. The subject locations were numerically coded and computer-analyzed to determine the pen locations of each *S* and the weekly mean distance from each type of partner. The inter-animal distances were based only on those occasions when *Ss* were recorded within the same pen. The Mann-Whitney *U* and X^2 Median Test were used to evaluate the homosexual *vs.* heterosexual distances. Trends across test weeks were tested by the Friedman test (Siegel, 1956). Hormonal effects observed in Study I were analyzed using repeated-measures analyses of variance.

As an index of aggregation, the percentage of males and females in each pen was determined for each diagram. To assess statistically the degree of homosexual and heterosexual aggregation, a criterion of at least an 80% aggregation of same-sex subjects in either pen was employed. The binomial expansion was then used to evaluate the probability of obtaining the observed number of criterional aggregations. To assess heterosexual segregation a criterion of at least 80% of males and females in opposite pens was employed and similarly evaluated.

Studies II, III, IV

Determinations of homo- and heterosexual aggregations and segregations were obtained through the use of the pen diagrams and analyses described for Study I. Inasmuch as the observations in Study I failed to indicate any significant difference between A.M. and P.M. observations, the diagrams for studies II, III, and IV were completed three times per observation day, three days per week, all during late afternoon. In order to provide pertinent behavioral data on the patterns of interaction within and between the sex and age groupings additional behavior samplings were obtained in Studies II, III, and IV. These samples involved 100 s of continuous observation of each *S* of the group, in random order, during which time the frequency and duration of a variety of pre-defined behavior patterns were recorded. These observations accompanied the completion of diagrams on each observation day and thus each *S* was observed for 300 s/week. Inasmuch as overt aggression was rare, the two opposing behaviors which were most directly pertinent to the observed spacing patterns were, (1) huddling: a subject sitting

crouched with its tail curled to its shoulder, while maintaining passive body contact with a partner; and (2) displacement: one subject moving at least 26 cm in immediate response to the approach or aggressive behavior of a partner.

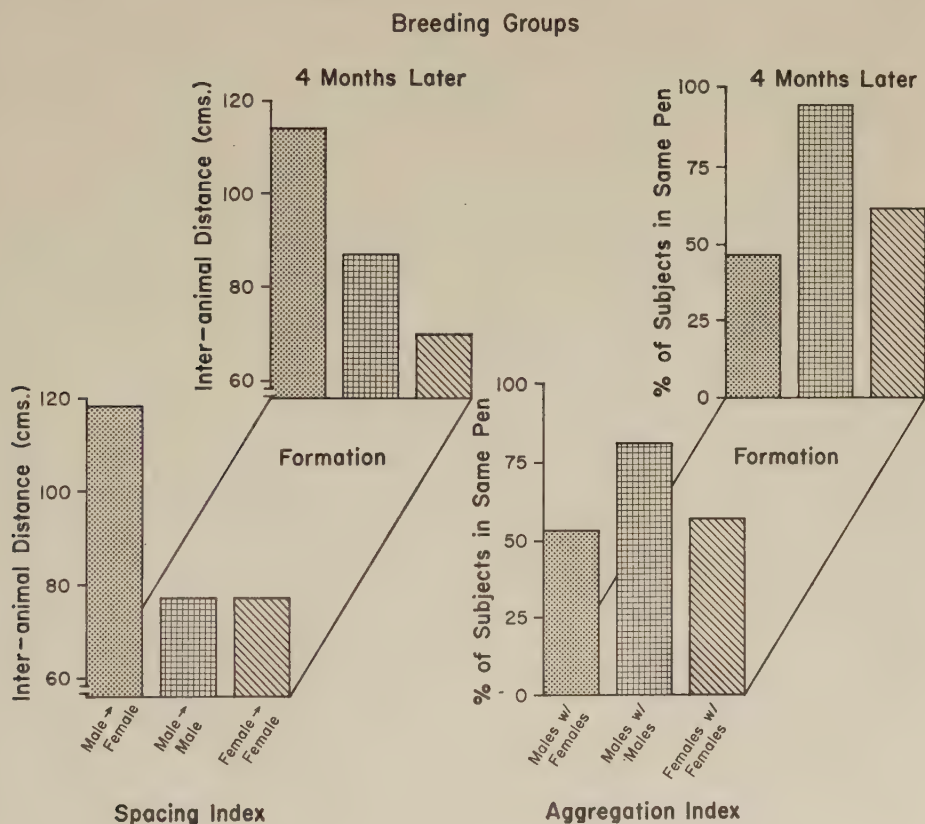
It should be noted that with subgroups of equal size (N), a member of a given subgroup has $N - 1$ of its subgroup and N members of the other subgroup with which it can interact. For example, in a group containing five males and five females, each male has four males, and five females as potential partners. Thus, within-subgroup scores must be adjusted with regard to between-subgroup scores before any valid evaluations can be carried out. All data presented in the current studies were adjusted in this manner.

5. Results

Study I

Analysis of the location diagrams of Study I showed that animal utilization of the two pens and the perches within each pen was consistent and systematic. As reflected in Figure 2, during the first three weeks following group formation, the Aggregative Index for males in both groups was 82%. Four months later this aggregative behavior was even stronger and an average of 96% of the males aggregated within one pen. Male

Figure 2. Inter-animal distances and aggregative indices for the breeding groups (Study I) for the first 3 weeks of group formation and a 3 week period 4 months later.



aggregation was significant in all weeks ($P < 0.01$; Binomial Distribution). The female subgroups, however, showed greater mobility between both pens and their Aggregative Index initially reached only the 58 % level. This score changed only slightly in the following four months to 62 %. This female index reflected the fact that several females in each group were rarely observed in the same pen as the aggregated males while the remaining females utilized both pens. The interactive effect of these male and female distribution patterns resulted in an intermediate level of the male-female Aggregative Index ranging from 53 % initially to 43 % four months later. Employing the stringent criterion of this study, this level of heterosexual segregation across the two pens approached but failed to reach significance.

The sexual segregation reflected in the Aggregative Indices was much more strongly evident in the spacing of male and female subjects within the same pen, i.e. the Inter-animal Distance scores (see Figure 2). An examination of the distance scores for intact males and females indicated no overlap of the distribution of homosexual and heterosexual distances in either the formation or subsequent observation periods. During the formative weeks there was an average of 78 cm between same-sex animals compared to 119 cm between males and females. The observed sexual segregation was particularly remarkable because there was considerable reproductive behavior during these weeks. Thirteen of the 16 intact females became pregnant during this period. The spacing pattern for both the males and females did not change significantly in the following four months, i.e. during mid-pregnancy, as homosexual distances averaged 79 cm and heterosexual distance averaged 114 cm.

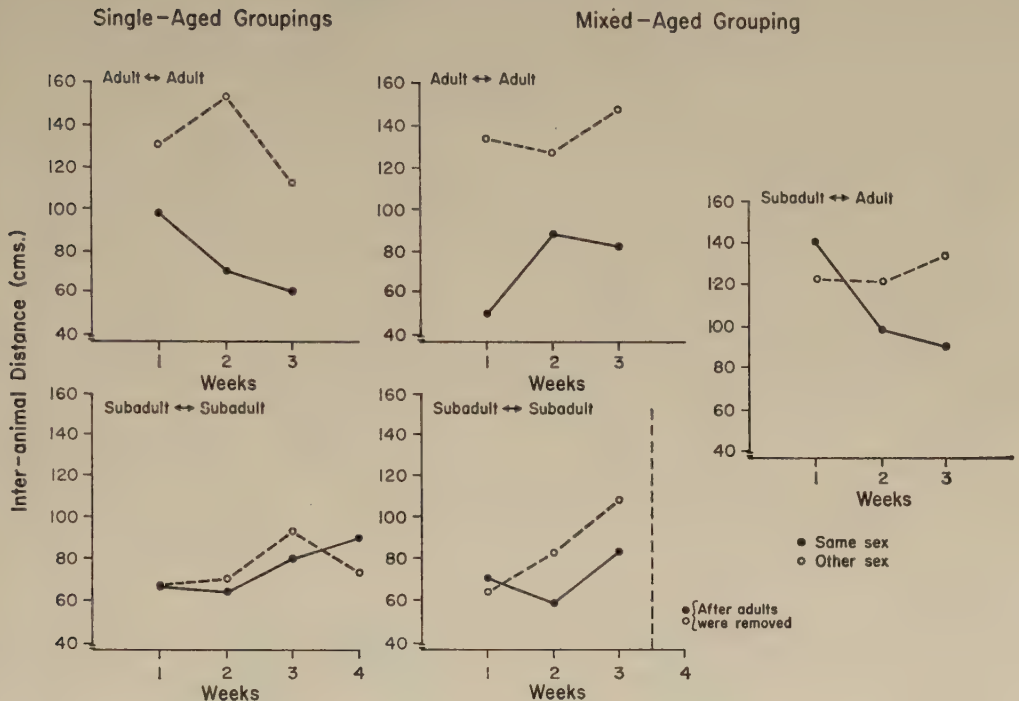
Although reproductive activity did not seem to affect the overall spatial pattern of males and females, endogeneous hormonal status appeared to have had some small initial effect. In each group, the castrated males compared to their intact counterparts were initially 21 cm further from males ($F = 12.4$; d.f. = $\frac{1}{20}$; $P < 0.01$) and 16 cm closer to females ($F = 3.8$; d.f. = $\frac{1}{70}$; $P < 0.06$). This difference in spacing by castrates was not evident in the Aggregative Index at any time, i.e. the castrates generally were observed in the same pen as the male cluster, and initial differences in distance scores had completely disappeared by four months later. The ovariectomized females of the two groups were not significantly different from the intact females on any distance measure at any time.

Study II

In Study II, the spatial segregation found amongst male and female adults in Study I was observed again but for a smaller group in the same environment. The Study II group which contained only five members of each sex did not show either significant homo- or heterosexual distributions between pens, i.e. the Aggregative Index. Nonetheless this group revealed a segregation pattern for the within-pen measurements which was quite similar to that observed in Study I. During the three weeks following group formation, the same-sex distance averaged 76 cm, whereas the opposite-sex distance averaged 133 cm ($P < 0.01$) (see Figure 3). Opposite-sex distances remained consistently large throughout the three weeks of observation. Same-sex distances within both the male and female subgroups on the other hand, continued to decrease sharply throughout the study, dropping from 98 cm initially to an average of 61 cm by the third week.

These indications of marked sexual segregation in the distance scores were supported

Figure 3. Median distances between subjects of the same sex (males w/males and females w/females) and the other sex (males w/females) during each week of observation. "Single-Aged Groupings" designates Studies II and III and "Mixed-Aged Grouping" indicates the data of Study IV.



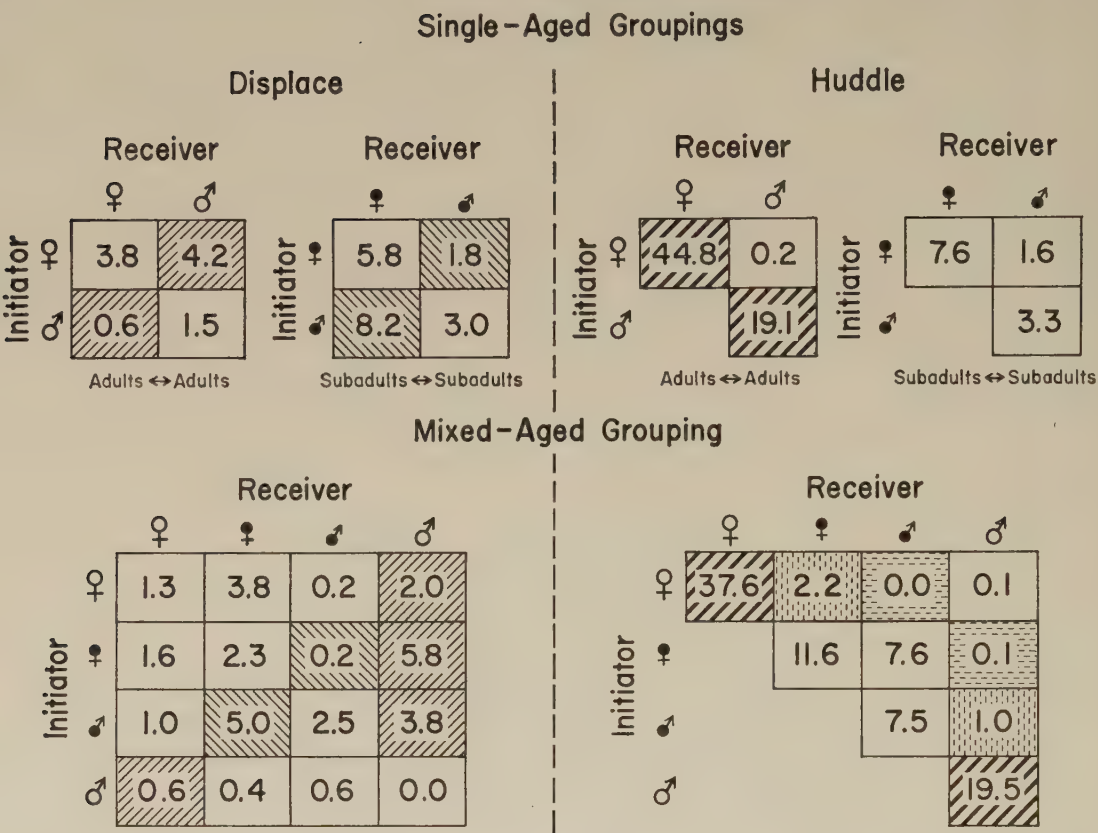
by the results of the behavioral observations (see Figure 4). Huddling between males and females was virtually nonexistent. Within-sex huddling scores on the other hand were relatively large, particularly amongst the females. The female huddling scores were more than twice those of the males, with no overlap in the distribution.

The maintenance of the relatively larger heterosexual distances was largely the result of intermittent but consistent female displacement of the males (see Figure 4). Each male received more female displacements than he initiated across the three weeks of observation. Furthermore, observation indicated that although female-female displacements were also somewhat frequent, displaced females returned relatively rapidly whereas males sustained their separation from the rejecting females.

Study III

The data of Study III indicated that the subadult subjects did not manifest the adult segregation pattern. As indicated in Figure 3, the differences in distances between subadults of the same-sex and opposite sex were only minimal—an average of 75 cm compared to 76 cm. Huddling between all *Ss* was relatively low and nonsegregated as indicated in Figure 4. Only two females accounted for most of the female-female scores and four of the five males engaged in some huddling with females. Thus the ratio of heterosexual huddling to homosexual huddling was considerably higher than for the

Figure 4. The mean score per subject for the frequency of displacements and the percentage of time spent huddling. Initiating subjects are indicated on the vertical axes and recipients on the horizontal. Larger, open symbols refer to adult males and females; smaller, closed symbols refer to male and female subadults. Data from Studies II and III are presented under "Single-Aged Groupings" and data from Study IV under the heading "Mixed-Aged Grouping". Shadings are intended to facilitate various age-sex comparisons.



adults. Displacements, though relatively more frequent in the subadults than the adults, occurred primarily in the context of play interactions and did not result in sustained separation of the subjects.

Study IV

This study involved a combined group composed of the adults of Study II and the subadults of Study III. The adult animals continued to maintain their original social pattern, locating themselves an average of 74 cm from same-sex adults and 135 cm from opposite-sex adults. As reflected in Figure 4, it is noteworthy that homosexual and heterosexual adult huddling was also maintained at levels quite similar to those observed in Study II. Adult females continued to displace adult males and the reverse was rarely observed. In fact males generally were displaced by all classes of subjects and did not actively displace others.

In the presence of the adult structure, a sexually segregated subadult distribution emerged. As indicated in Figure 3, in week one, same-sex and opposite-sex distances among the subadults did not differ. In weeks two and three however, the opposite-sex scores amongst subadults were significantly higher than their same-sex scores ($P < 0.01$). By the third week, this trend resulted in an average opposite-sex distance of 108 cm, compared to a distance of 84 cm between the same-sex subadults.

This change in the subadult distribution seemed primarily due to their pattern of interaction with the adult animals. Beginning in the second week, the subadults overcame their initial fear of the adults and increasingly approached them. From this point on, two factors influenced the development of the social structure which ultimately emerged. First, the subadults, primarily the females, frequently approached the adults. Secondly, the adults responded differentially to the approaches of subadults of their own and opposite sex. Adult females were ultimately more tolerant of subadult females than subadult males. The adult males, though generally avoiding all other subjects, appeared more accepting of the subadult males. As a result of these factors there was a significant decrease of 50 cm in the distances between the subadults and adults of the same sex ($P < 0.01$). There was a correspondingly significant increase of 11 cm in the distance between subadults and adults of opposite sex ($P < 0.02$).

Displacement scores between age-sex groupings did not provide a simple indication of the changing spatial patterns. Subadult females received more displacement from adult females than did subadult males. However, this was a reflection of the subadult females' sustained efforts to approach the adult females and return repeatedly. Subadult males, on the other hand, when rebuffed, rapidly decreased their approaches to females. Adult males generally avoided contact with subadults but were more readily displaced by subadult females than subadults males. These forms of interaction ultimately led to relatively greater proximity between the subadults and adults of the same sex. As a further outgrowth of these displacement behaviors, subadult males and females never huddled with opposite sex adults. However, some degree of huddling, increasing over weeks, did appear with same-sex adults.

The emergence of these mixed-age, same-sex groupings was the basis of the increased sexual segregation among the subadults. As indicated in Figure 3, when the adults were removed, the subadult pattern of apparent segregation immediately reverted to the heterogeneous clustering previously observed in Study III.

6. Discussion

The analysis of distances maintained between adult squirrel monkeys reflected the balance between the tendency of males and females to disperse from one another and form cohesive homosexual clusters, and their continued heterosexual attractions. Thus, the data clearly indicated consistently greater heterosexual than homosexual spacing within a pen. However, the failure of the two sexes to separate maximally between the two available pens, as reflected in the insignificant levels of the heterosexual Aggregative Indices, was indicative of the continued motivation of males and females to remain integrated within a sphere of potential interaction. The homosexual orientation did not appear to be dependent on endogenous hormonal levels since the segregated pattern was observed in intact adults during both the mating and mid-pregnancy phases of their annual reproductive cycle. In addition, gonadectomized males and females also showed

this social pattern. The presence of a normal adult social structure in the Breeding Groups may have facilitated the same-sex preferences of the gonadectomized animals since a previous report suggested that following gonadectomy squirrel monkeys lose their social orientation (Alvarez, 1969).

The impact of a stable social structure on social orientation was also apparent in the observations of subadult squirrel monkeys. Subadults did not reveal a consistent sexual organization by themselves. However, these subadults were strongly attracted toward adult monkeys when available and, through a process of sexual selection by the adults, readily affiliated themselves with the adult segregated structure. As a result the subadults were increasingly proximal to adults and subadults of their own sex and farther from opposite-sex animals. These findings suggest that younger monkeys initially develop the adult pattern through a socialization process involving the redirection of social attachments from age-peers of both sexes to animals of the same sex.

Subadult females showed more readiness to develop interactive and cohesive patterns with same-sex adults and this predisposition may reflect the stronger social attachments of adult females. Adult females play a major role in affiliative and agonistic interactions which determine the spatial relations between adult monkeys. Adult females manifested high levels of both socially cohesive and dispersive behaviors. Huddling, which was virtually restricted to same-sex partners in adults occurred significantly more often in females. Moreover, females showing no fear or subordination to males were more active in displacement behavior and frequently caused the males to flee. This displacement of males allowed females freer use of the spatial environment.

These results complement a recent emphasis on the important contribution of female Primates to maintaining social order and transmitting social dominance (Koyama, 1967; Lancaster, 1973). In addition, these data support the suggestion that females may have been the more socially aggregative members of early Primate groups and that the evolution of integrated male-female groups may have involved the addition of males to multi-female assemblages.

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D. Munkenbeck
Fragaszy

G. Mitchell

*Department of Psychology,
Department of Behavioral Biology,*

and

*California Primate Research Center,
University of California, Davis,
Davis, California, U.S.A.*

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Infant Socialization in Primates

This review considers evolutionary trends, functions, stages, and current issues in Primate socialization. The concept of social "set" is discussed in the context of the interactional nature of socialization, where the infant is regarded as a primary effector in its own socialization. Laboratory approaches and measurement techniques are reviewed briefly.

Like humans, most other Primate species live in organized groups. Those of us involved in attempting to understand the proximate and ultimate causes and functions of group life in Primates have tried a variety of research approaches. The research strategy upon which we will focus here is the study of infant socialization, the process by which a new individual comes to play its part in maintaining the life-style of the particular group into which it is born. The proper socialization of the infant Primate (and other social species as well) is necessary for the maintenance of the group across generations. There is great inter-specific variability in Primate socialization processes, but equally striking is the remarkably efficient and predictable way in which the infants develop into participating group members.

1. Functions of Socialization

The infant's development into a participating group member can be viewed at the level of the individual, group, or species. Divisions of research along disciplinary lines—psychology investigating the individual and anthropology the species—are disappearing (Poirier, 1972; Williams, 1972). The vigor socialization research is currently enjoying is partially attributable to an eclectic approach.

Socialization determines whether or not a *species* maintains or increases its fitness. At the *group* level, Primates usually have stable, well organized patterns of interaction (Kummer, 1971; Altmann, 1967). These patterns come about through socialization. Transmission of "culture" to a new generation within a group as described by Itani (1958) and Kawai (1965), illustrates the possible importance of socialization (Burton & Beck, 1972). At the level of the *individual*, socialization functions to form and maintain affiliations among individual group members and to properly prepare the infant's behavioral repertoire so that appropriate stimuli elicit appropriate responses.

2. Socialization as a Process

In terms of the *group*, socialization involves learning on the parts of both the infants and other group members. Individual recognition is an important early task, and there are many other tasks to be learned as well (e.g. individual differences in temperament,

responses toward other group members, etc.). For the *individual* infant, proper social development involves the elicitation and practice of a full repertoire of social responses (Mason, 1970; Hinde, 1971). Each group member may be seen as having several possible "roles" in the socialization of an infant. These "roles" are determined by that individual's motivational and stimulus properties for a particular infant. These properties clearly change over time as the infant develops new physical and cognitive skills. Because these interactions change with time, it is misleading to pigeon-hole individuals as having one specific "role" in an infant's socialization.

3. Evolutionary Aspects

Selective factors and adaptive responses to them are responsible for discernible evolutionary trends. Selection can alter phenotypic fitness. Scott & Fuller (1965) have shown in dogs that selection can in fact alter behavioral traits and motivational factors which affect socialization. Such multiply-determined behaviors as approach and social investigation are affected by genetic factors, and these traits have undoubtedly been altered during Primate evolution.

There are general evolutionary trends in the socialization of Primates. "Intelligence", admittedly an amorphous, ambiguous concept (Thorndike, 1911; Nissen, 1954), may be usefully viewed as flexibility in behavior systems—i.e. the potential for learning (Mason, 1971). Behavioral flexibility is tied to group living in Primates. The length of the socialization period, and the complexity of learning involved, increase through the order Primates. As the behavioral system becomes more open (i.e. more potential for change exists), learning plays a greater role in the expression of genotypic potential. Socialization provides for the orderly acquisition and expression of responses appropriate to the particular circumstances affecting each new individual. There is an evolutionary trade-off: as flexibility is gained, more steps enter into the maturation process, and the socialization process becomes vulnerable to maladaptive adjustments. Laboratory researchers have been investigating the potential for such maladaptive responses. The isolation studies at Wisconsin and current cross-rearing experiments are examples (e.g. Harlow & Harlow, 1965; Maple, 1973; Mason & Kenney, 1974; Mitchell, 1968*b*).

Another trend in Primate evolution is an increase in infant dependence. Infants are increasingly less mobile, less physically developed at birth, and correspondingly more dependent on caretakers for a longer period of time as one surveys from prosimians through apes. This means that there is an increasing capacity for nurturant behavior on the part of other group members. Observations have frequently been made on extraordinary responses towards disabled immature individuals (Lindburg, 1969; Berkson, 1973; Rumbaugh, 1965). In one study by Berkson (1973), nearly blind rhesus infants were accepted by their peers and exhibited adequate social behaviour. These disabled infants were protected by group members at an age exceeding that normally observed. These extraordinary nurturant responses are indicative of an increased overall potential for care-giving behaviors. Other obvious examples involve adoptions of orphaned infants (e.g. Kaufman & Rosenblum, 1967).

One evolutionary aspect of socialization about which we can presently *not* generalize is species-typical social structure. In addition, the particular individual traits on which socialization experiences exert their effects are not clear. Basic social preferences, responses, and arousal tolerances have been investigated in the laboratory (e.g. Sackett,

1970; Mason, 1961c; Redican *et al.*, 1971; Mason *et al.*, 1971). The laboratory research that has been done is a step in the right direction, but has not yet enabled us to state with confidence whether the socialization process, or species preference differences, are the determining factors in the development and maintenance of species-typical social organization. Most field research documents the existing preferences (e.g. females often cluster together, males often avoid each other) without attempting to trace their ontogenies too closely. Hans Kummer's (1971) perceptive field-laboratory work with baboons and patas monkeys is an example of how illuminating results can be achieved on problems of preference and social organization, albeit he was not concerned with socialization *per se*.

4. Stages of Socialization

Socialization may be viewed in maturational stages. What follows is a discussion of behavioral stages utilizing macaques for consistency and brevity.

The first stage, from birth to approximately 1 month of age (in rhesus) may be called reflexive (Harlow, 1965). The infant initially responds in an indiscriminate way towards social objects. Excessive arousal induces a clinging response, which leads to arousal reduction (Mason, 1971). Prevention of clinging causes distress, accompanied by vocal and physical responses. During this period the infant forms a deep and abiding emotional attachment to its mother (or mother-surrogate), and this attachment is critical to the infant's subsequent broader socialization experience. The infant is no longer simply dependent, no longer restricted to reflexive behaviors. The formation of an emotional attachment to a specific social stimulus implies that the infant has developed the capacity for perception of "object permanence" (Piaget, 1952; Mason, 1970). The development of object permanence probably precedes the development of the next major social period, that of social exploration.

There are reasons for the early reflexive period in Primate development. The infant's biological needs must be taken care of in an orderly fashion. The reflexive patterns which maintain proximity and contact between mother and infant are well designed to ensure that the infant will be fed and comforted. As the infant develops motor and cognitive skills, however, this emotional/biological attachment is apparently no longer sufficient to satisfy the infant's need for stimulation. When the infant is ready for additional social stimulation, it turns to the non-mother environment. It begins independent exploration (Jensen *et al.*, 1967; Chevalier-Skolnikoff, 1971). The reflexive period of socialization establishes a satisfactory relationship with the mother but is limited in that the infant is often not interacting with the mother on a voluntary basis, nor does it learn adult communication signals from her. Flexibility *does* develop in the mother-infant dyad, but it first becomes obvious in social relationships with other group members.

When the infant makes efforts to explore the environment on its own, it becomes capable of recognizing other individuals and develops responses appropriate to each individual encountered. It develops a complete social network—a set of interactions with all group members (Simonds, 1974). Although the infant's social experiences are still influenced by maternal status, temperament and social contacts (Sade, 1967; Koford, 1963), the infant can now interact voluntarily. It is a participating group member, as opposed to a member of a closed dyad. It can now interact with its mother in a more social way as well (Chevalier-Skolnikoff, 1971), and this new bond with the mother soon becomes broadly based, and pervasive in its influence. One may see the infant as now

possessing a sense of security at a distance. Direct physical contact is no longer essential to maintain satisfactory levels of reassurance. The infant carries around with it an internalized source of security: the knowledge of the mother's availability in times of need. The infant still seeks emotional security from the mother at ages when it is physically well able to cope for itself (Lindburg, 1971).

Matrilinial kinship ties are an important (perhaps primary) source of group affiliation (Sade, 1965; Lindburg, 1972; Koford, 1963). One may view the continuing strong attraction of the infant to the mother as the primary thread in the social fabric. Furthermore, the mother is an active participant in the protection/reassurance pattern within the dyad. Her behaviors, such as retrieval, restriction, or protection from other adults or older juveniles support the infant's immature response patterns. In this way, the mother maintains her position as a focal object in the organization of the infant's socio-emotional behavior. If one assumes that attachment requires a certain exposure time (Cairns, 1972; Hoffman & Ratner, 1973), the mother ensures by her restrictive behaviors that the infant will become less attached to animals other than herself for many months after birth. Physical protection of the young infant is necessary; undoubtedly this is a primary function of protective behaviors. The restriction of attachment is probably a secondary rather than a primary outcome, but it is one that is important.

The adaptive functions of a continuing strong mother-infant relationship for the individual are complex and have not been investigated in detail. Why does a young animal continue to rely on earlier coping mechanisms (e.g. reassurance from the mother) even when others have become available to it? The young individual is probably not efficient at controlling its arousal levels by itself until long after it is eating solid food and displaying a complete behavioral repertoire. Even though the behavioral repertoire may be complete, perhaps the requisite learning of behavioral consequences has not yet occurred. For example, the young juvenile may have given and received threats many times in peer interactions, yet when threatened by an adult, may respond in an immature fashion instead of giving the appropriate adult appeasement gesture.

As the infant develops a network of social contacts, play groups develop. The infant chooses to associate with like-aged (and eventually like-sexed) peers. New social responses develop, including sexual patterns, appeasement gestures, aggressive behaviors and so forth. This period of intense playful social interaction permits the repeated performance of many elements of the social behavioral repertoire. Development of social communications is a necessary element in the orderly socialization process.

These generalizations have not considered many important elements in socialization: continuing mother-infant interactions, other adult animals, sex differences and so forth. The reader is referred to Poirer (1973), Mitchell (1968*a*), Hinde (1971, 1972), Rowell (1972), or Mason (1970, 1971) for more detailed discussions of these other factors.

5. Current Issues: Social "Set"

We will focus here on a few current issues in socialization research, again primarily limiting our examples to macaque species. These examples will concern the infant's part in its own socialization, since there is often a tendency to regard the infant as a passive "receiver" of socialization (see Rosenblum & Kaufman, 1967). We propose that the infant be viewed as developing an internal, consistent approach to social interactions (i.e. a social "set"). This concept will be expanded below to apply to several different

aspects of socialization. The socialization process is inherently interactional. The infant brings its own equipment for socialization into the world with it. Group members act on that original material to develop its expression, but they can not create new responses or *force* expression of existing ones. The mother may provide the infant with an opportunity to perform many behaviors, but behavioral deficits resulting from manipulation of social contacts are not due to a lack of experience with specific individuals *per se*, but rather to the lack of opportunity for the infant to express, and develop by itself, its full behavioral repertoire (Mason, 1971). An infant's biological sex is of importance in this regard.

It is true that male and female infants are treated differently by adults (Mitchell, 1968a; Simonds, 1974). Adults inspecting the genitals of new baboon infants continue to show interest in the male's penis or scrotum after they no longer are so interested in the female's external genitalia. It does not seem warranted, however, to state as Rowell (1972, p. 146) does, that the adults have "established a pattern of *interaction* with the infant after inspection of genitalia" (italics added). It seems more likely that differences in treatment of the two sexes by their mothers and other group members are due more to intrinsic behavioral response differences between the sexes. Mothers are, at first, more protective of female infants, later on being more punitive with male infants. Work done by Goy and colleagues (e.g. Goy & Phoenix, 1972) has shown that existence or absence of circulating prenatal androgens has pervasive organizational influences on behavior. Genetic females injected with testosterone propionate before birth develop masculine patterns of threat, mounting, rough and tumble play, and other sexually dimorphic behavior patterns long before hormonal differences appear at puberty. Early differences in behavior due to sex are caused by *similar* experiential factors acting on *differing* sensitivities (due to presence or absence of prenatal androgens).

Parental input is important, however. Brutal mothers produce more aggressive infants, punishing mothers produce anxious, dependent infants, permissive mothers produce exploring, playful infants and so forth (Sackett, 1970; Rosenblum & Kaufman, 1968; Mitchell, 1970).

Socialization has cognitive attributes as well as emotional-motivational ones. Early in its life, the infant develops a characteristic set of responses for dealing with excess levels of arousal or, conversely, inadequate levels of stimulation. Isolate-reared infants provide their own stimulation by self-rocking, self-sucking, self-threatening, etc. (Mitchell, 1970; Sackett, 1968; Mason, 1968). Once a pattern of coping with environmental and internal demands has been developed, rapid changes in response patterns are not likely. An infant which has had satisfying relations with the mother will carry this positive social set into its new relationship. Such an infant is more likely to be positively responsive to its new peer than is an infant which has had to struggle to maintain an acceptable level of contact. This is another context in which one may view the infant as socializing (affecting its interactional partner) as well as socialized (Rheingold, 1969).

Thus, the isolate infant can be viewed as reacting abnormally to social contacts not only because of fear of novelty and communication inadequacies (these are certainly major handicaps), but perhaps also because it has not developed a satisfactory social set. A "mother" does not provide adequate opportunities for satisfaction of the infant's basic needs, forcing the infant to go to extreme lengths (self-stimulation) to satisfy these needs. Mason (1968) has shown that infants reared with movable and moving surrogates not only did not develop stereotyped rocking and abnormal postures, they were also

more exploratory and playful when given opportunities for social contact than were their isolate analogues. The persistence of a set can be seen in Chevalier-Skolnikoff's (1971) findings that stump-tail macaque infants continued to interact with their mothers using infantile signals even after they had developed adult visual signals and used the adult signals frequently with all other group members. Current work being conducted on adult male-infant pairs in rhesus monkeys (Redican & Mitchell, 1973) can also be viewed in the context of set. Although adult males rarely interact with infants to any appreciable extent in the wild (Lindburg, 1971), they perform admirably as social companions in the laboratory. Male-raised infants (one year of age) appear to be as socially well adjusted (on the basis of home-cage observations) as mother-raised infants. There are interesting differences, however. Male-infant bonds do not seem to wane as the infant matures. Up until now the males and their infants have continued to increase social contact with one another, spending much more time in rough and tumble play. Normal sex differences in attachment behavior have appeared in these pairs, indicating once again that the infant's built-in behaviors go far toward determining the course of socialization.

Other findings concerning social set development involve the subtle deficits exhibited by isolate-raised juveniles in a group situation (Anderson & Mason, *in press*). Rhesus monkeys given peer experience during infancy are able to conduct social interactions with two or more other participants concurrently. Individuals lacking this experience are able to react on a one-to-one basis only. Their social relations lack the rich give-and-take, multiple participation of their more experienced peers.

6. Experimental Approaches

Let us now turn to current experimental approaches used in studies of infant socialization. Differences exist within as well as among Primate species in almost any behavior category one might choose to name; however, distributions often overlap to an appreciable extent. Increased unpredictability is one natural result of increased behavioral flexibility at all levels of development. Socialization research must deal with this problem, as must all Primate behavioral work.

The control of the young infant's social environment is one laboratory approach to the study of socialization. Social contacts have been restricted by rearing in total isolation, alone with the mother, alone with a peer or peers, with changes in mother, in nuclear "families", with forced adoptions, in rearing with other species and so forth. Environmental control may extend to non-social aspects of the environment, such as control of complexity of visual stimuli or opportunities for non-social play (e.g. Sackett, 1970). The goals of environmental control are first to isolate contributing factors and then to put the pieces of the puzzle together for a clear picture of "normal" socialization. There is a flaw in this, for the sum is more than its parts. Dyadic interactions do not re-present the full social repertoire. In addition, environmental restrictions have pervasive influences on other aspects of behavior than the particular one under study. When these limitations are kept in mind, this kind of laboratory research contributes to our understanding of socialization.

Separation from social contact has been one fruitful strategy of the laboratory behaviorist. Robert Hinde and colleagues (e.g. Hinde, 1972; Hinde & Spencer-Booth, 1971; Spencer-Booth & Hinde, 1971) have used the rhesus infant as a human model in

their studies of long- and short-term behavioral effects of separation from the mother. Suomi, Harlow & Domek (1970) have used repeated peer-separations to induce severe behavioral abnormalities. Other researchers have used separation as a technique to determine strength and specificity of attachment to the environment, the mother-surrogate, or the social partner (e.g. Brandt, Baysinger & Mitchell, 1972; Candland & Mason, 1969; Preston *et al.*, 1970; and others). Separation has also been used to determine group responses to an abandoned infant (Hinde, 1971; Kaufman & Rosenblum, 1967).

Deprivation studies have involved various environmental controls: absence of mother, peers, other adults, or all social objects. Dyad experiments are common deprivation studies. In a dyad the infant is forced to concentrate its social activities on a limited social resource. For example, one current dyad experiment involves pairing rhesus infants with adult male conspecifics. Other interesting deprivation studies have included studies of social and cognitive development (Mason, 1960, 1961*a,b*; Mason & Green, 1962; Harlow & Harlow, 1965; Seay *et al.*, 1962) as well as studies of marked abnormalities resulting from deprivation (cf. Mitchell, 1970; Sackett, 1968).

The nuclear "family", used by Margaret Harlow and colleagues, represents an interesting modified deprivation approach. In this design, families of rhesus (mother, father, infants) share common living quarters. The infants have a central "play-pen" to which only they (infants) have access. Furthermore, the infants have access to non-parental adults (Harlow *et al.*, 1971). An earlier study used a similar play-pen design as a way to control retrieval abilities of the mothers while permitting infants free peer contacts (Hansen, 1966).

Still another research approach involving control of the social environment has great potential for resolution of socialization issues. This approach is cross-rearing (i.e. rearing an infant with a member of a different species). This approach was used by Kuo (1930) and more recently by Kaufman & Rosenblum (1968), Mason & Kenney (1974) and Maple (1973). One goal of this approach is to find out how much of the infant's social development may be due to species-specific experiential learning, and how much may be attributed to general Primate social experience. In other words, how flexible are the Primate social systems with which we are dealing?

Current work by Mason & Kenney (1974), rearing infant rhesus with dogs, promises to point up new aspects of cognitive social development. Rhesus infants of varied backgrounds have successfully formed specific strong attachments to dog companions, even preferring them over a conspecific peer in a choice situation. Research now under way on these dog-reared monkeys will examine differences in exploration and cognitive skills resulting from various social arrangements and particular play and task-solving experience. It is hypothesized that infants having an "enriched" early history (i.e. a dog companion with which the infant explores the play area), and having an opportunity to develop problem-solving skills, will carry their exploring, solving set with them into other tasks. This would be in contrast to infants who must explore on their own or to those who have less problem-solving experience.

Maple (1973) has recently begun cross-rearing studies with year-old baboon-rhesus pairs. Early observations indicate that once initial communication misunderstandings have been overcome, the infants interact in positive ways, including clinging. It will be most interesting to see if their future sexual behaviors will be addressed to conspecifics or, if given the opportunity, they would prefer their cagemate species in a group situation. These animals were wild caught yet their previous attachments apparently have not

prevented the development of new, strong attachments to an alien species. These results support similar findings of reversibility of infant attachments in Mason & Kenney's (1974) dog-monkey experiments.

7. Research Techniques

There is little standardization of categories or techniques used in measuring Primate behavior. Altmann (in press) reviewed current popular sampling techniques used in observational studies of social behavior, and listed seven major types. Each of these different methods introduces different sources of bias, and each is best suited to specific kinds of research. When reviewing the literature on socialization research, the problem of comparing data obtained using different techniques becomes unavoidable. In the consideration of research techniques, we will focus on three basic methods: preference tests, dominance tests and an analysis of roles.

Preference tests have been used to measure the strength and specificity of an attachment. When an animal is placed in a situation where it must actively choose to go near or orient towards a choice animal, it displays preference for (i.e. greater time spent near) the animal for whom it has the greatest attraction. This technique has been used by Mason & Kenney (1974), by Sackett (1970), by Seay *et al.* (1970), and by others. Findings indicate, for example, that isolate infants prefer other isolates over more socially experienced peers; that isolate-reared mothers avoid their own infants, but feral mothers prefer their own infants, and so forth. In using a method measuring orientation and proximity, the experimenter must be careful to distinguish positive from negative attraction (i.e. affiliation *vs.* hostility). For a more complete description of this method and results, see Sackett (1970) or Mitchell (1972).

Role analysis is another technique, and Robert Hinde (1971) has considered in some detail the problems and advantages provided by it. He notes, quite rightly, that the term "role" has come to have diverse meanings which are not distinguished in the literature. It may mean a quantitative description of behavior in a particular sample of animals (e.g. an age/sex class, such as male juveniles), a quantitative description of behavior with a particular consequence (e.g. dominance), or the behavior of an animal engaged in a particular action (e.g. feeding *vs.* standing guard).

Despite this confusion, efforts to work with the role concept *have* been productive (Jensen *et al.* 1967; Hinde, 1971). The roles of the mother and infant in maintaining proximity have been investigated. Hinde (1971) has attempted to show that age changes observed in infant independence (time off the mother and at a distance from her) are due mainly to the mother's behavior, even when the infant is very young.

Dominance determinations are popular in studies of group relations. In socialization work, the stability, rigidity, maintenance and normality of status hierarchies are considered indicators of the social well-being of individuals in a group. Dominance relations are said to be an obvious key to group interactions, but what is "dominance"? Different measures of dominance result in different hierarchies, and repeated observations on the same group, using the same methods, frequently produce switches in rank order (e.g. priority of access to food may be differently ordered than right-of-way on a perch or tree). The presence of a human observer can also affect the results of a dominance test (Maple, 1974). In some natural groupings, motherhood and infancy are accorded special status, further complicating the picture. In addition, coalitions among individuals

in larger groups may produce different results than simple pair interactions (Lindburg, 1971).

General statements can be made concerning dominance abnormalities in socially deprived, isolate-raised, or strange peers (Mason, 1961*b*; Sackett, 1968; Mitchell, 1967, 1968). Deficits in the early learning of skills (visual and auditory communication) are implicated in an inability to develop stable dominance relations (Sackett, 1968; Clark, 1968; Miller *et al.*, 1967; Brandt & Mitchell, 1973). Socially deprived monkeys have less complex and less stable status relationships than their socially experienced counterparts (Anderson & Mason, in press). Dyadic observations have also revealed less stability in dominance relations in deprived monkeys (Mason, 1961*b*). Deprived individuals are not as able to "enlist" aid from companions during dominance interactions as are socially experienced individuals. Experienced subjects include fellow group members in their interactions in a more complex way than do deprived subjects, and in the wild, coalitions occur frequently during dominance interactions (e.g. Lindburg, 1971).

Researchers utilizing dominance measures report the reversibility of dominance-submissive behavioral deficits in *Macaca fascicularis* (Karrer & Dekker, 1973). Partial-isolation-reared young animals were observed during spontaneous group interactions, as well as during paired food-competition trials. During initial pairings, the subjects exhibited little dominance-submissive behavior and interactions were minimal. After two months of group living, however, pairs exhibited well-defined dominance relationships, and pair relationships reflected the same rank order of the subjects as when they were in the larger social group. Social experience at a later age reverses at least some of the consequences of early social deprivation.

8. Summary

Socialization is a broad concept which includes the processes by which an individual comes to be a participating group member. We have considered various definitions and functions of socialization, some evolutionary trends, as well as some age-related stages and their functional significance. We have covered a sample of experimental approaches and measurement techniques.

Socialization researchers ask fundamental questions about the development of social behavior. In Primates, we are particularly interested in the development of species-specific behaviors, in the relationship between early experience and subsequent social behavior, and in the basic flexibility of the social learning system. Investigation of these issues is relevant to an understanding of Primate evolution. Complex social organization is one of the distinguishing characteristics of Primates. Knowledge of its evolutionary development, including the ontogeny of individuals, will give us greater insight into human affinities with our Primate relatives. As Kummer has pointed out, we must examine the "range of modification potential" (Kummer, 1971, p. 154), and this can best be accomplished through manipulation in laboratory settings.

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Chimpanzee Subsistence Technology: Materials and Skills

Beyond reviewing basic data on Primate technological behavior, the aim of this report is to document the nature of chimpanzee technical skills by examining some of the mental as well as physical expertise which chimpanzees bring to bear on subsistence activities. This task is approached along several avenues: first, an outline is drawn of current knowledge about chimpanzee subsistence technology throughout Africa; second, a sketch is made of technological variability in several chimpanzee populations; third, the results of a personal investigation into the skills needed by chimpanzees to probe for insects are provided; and fourth, a comparison is made of the baboon, chimpanzee and human techniques used to exploit termites as a food resource. Instead of focusing on the unique features of human subsistence technology, the report attempts to show that many technical skills are and probably were firmly rooted in Primate prehistory, well before the advent of the earliest hominids. An integrated model of technological achievements among extant Primates, based on a sample of African cercopithecids, pongids and hominid populations representing stages in a phylogenetic sequence, is offered as a foundation for reconstructing the gradual evolution of primate subsistence technology. This approach is intended to provoke contemplation and discussion among those investigators of human behavior and society who favor the thesis that the criterion of technology, together with the cultural transmission of technical skills, separates the human from the nonhuman Primates.

1. Introduction

Research on the technological capabilities of captive chimpanzees spans more than half a century. Studies on the ability of pongids to manipulate, assemble and modify objects for use in specific tasks range from the designed experiments conducted in cages by Köhler (1925) to the spontaneous behavior observed in compounds by Menzel (1972, 1973). It was merely a decade ago, however, that research on wild chimpanzees began to yield information on their technological performances in natural conditions (Goodall, 1964; Kortlandt, 1965).

The literature describing such technological achievements is now expanding at such a rate that all the data cannot be reviewed in this brief report. Thus, reviews of the "tool-using" and "tool-making" performances observed among nonhuman Primates and other fauna (Hall, 1963, 1965; Kortlandt & Kooij, 1963; van Lawick-Goodall, 1970) should serve as an introduction to the subject. Only the salient features of nonhuman Primate "technological behavior" will be considered here. My attention will center on the technical skills exhibited and on the materials utilized by chimpanzees living in natural habitats, and specifically on those attributes which occur in association with subsistence activities—namely, any behavior oriented, via technological extension, toward obtaining and/or preparing substances for ingestion. Due to this orientation, many other patterns of behavior involving objects (e.g. drumming on buttress roots, building nests with branches, displacement grooming with leaves) will receive only cursory attention.

Three main points underlie this limited focus. One, having completed nearly two years of work with chimpanzees in Gombe National Park, Tanzania, these field experiences

have inevitably funneled my interests and insights in the direction of naturalistic behavior. Two, laboratory research on the skills elicited from chimpanzees and other Primates can provide vital information about the behavioral and psychological *potentialities* associated with manipulation and modification of objects, but only field research can establish the extent to which these potential capabilities are actually *realized* in natural populations. And three, knowledge about the realized subsistence technology of extant chimpanzee populations may shed light, albeit indirectly, on the evolution of technical skills among Primates in general and among the early hominids in particular.

2. Contexts of Technological Behavior

In order to provide some comparative perspective to the study of chimpanzee subsistence technology, the general dimensions and contexts of both baboon and chimpanzee technical skills are outlined below. A sketch of technological behavior in these African genera is appropriate for the following practical and theoretical reasons: because (a) many populations within these genera have been thoroughly studied in field conditions (Baldwin & Teleki, 1972, 1973); (b) the basic subsistence patterns of baboons and chimpanzees are similar, both being omnivores that collect flora and prey on fauna, and their collector-predator habits can be ranked along a graded spectrum of diversity and complexity which integrate with human gatherer-hunter habits in the same African regions (Teleki, in press); (c) numerous populations of these genera live in areas that lie within or near to the African rift system, in habitats that range from arid savanna to rain forest, and thus inhabit geographical and ecological zones which were associated with hominid emergence (e.g. Pfeiffer, 1969); and because (d) these more than any other Primate genera have been cited as models for reconstructing the behavior, social life and subsistence habits of early hominids (e.g. Washburn & DeVore, 1961; Mann, 1972).

In comparison to humans and even to chimpanzees, wild baboons exhibit a distinctly limited repertoire of technological behavior. Although Primates in general tend to apply their technical skills mainly in contexts other than subsistence (Hall, 1963; Kortlandt & Kooij, 1963), the meager records of technical performance among baboons are in fact restricted to this one context. Marais (1969) observed chacma baboons break open hard fruits with stones; Kortlandt & Kooij (1963) reported accounts of baboons using objects to crush a scorpion before eating it, to widen the entrances of ant and termite nests and to stir up insects under rocks; and van Lawick-Goodall, van Lawick & Packer (1973) observed a baboon wipe her lips with a small stone after feeding on sticky pods. Several of these manipulative performances are similar in function and execution to those which will be described under chimpanzee subsistence technology, but the levels of sophistication routinely reached by chimpanzees, especially in modification and transportation actions, are qualitatively and quantitatively beyond those achieved by baboons. For example, when considering the many thousands of field observation hours spent with baboons during the past decade or so, this list is seen to contain a mere sprinkling of incidental cases which fall rather short of establishing baboons as technologically adept Primates. This sharp limitation is in some respects anomalous, for baboon subsistence patterns are in many other ways quite closely analogous to those of omnivorous chimpanzee and human populations, especially in predatory and hunting behavior (Teleki, in press).

Wild chimpanzees, on the other hand, occupy a firm position as the most technically skilled of all living nonhuman Primates, at least at the time of this writing. These

African apes exhibit a rich array of technological behavior that incorporates the manipulation, modification and transportation of many types of materials; and their varied, often highly sophisticated technical skills are applied in subsistence as well as in many other contexts, both agonistic and nonagonistic. Typical agonistic actions include shaking, flailing, dragging, throwing, hitting and thrusting with trees, branches, sticks, twigs, fronds, stones, earth clods, leaves and even food items (van Lawick-Goodall, 1970; Kortlandt, 1968). And nonagonistic technical skills are exhibited during food and water collecting, investigate probing, displacement grooming, nest building, body cleaning, solitary and social playing—situations in which stones, branches, sticks, twigs, vines, grasses, leaves and other materials are manipulated and sometimes modified to suit specific functions (van Lawick-Goodall, 1970). Chimpanzees are also known to transport certain objects for considerable distances, and to fetch objects from one place to another in order to perform some premeditated task.

Technological performances in contexts other than subsistence have been recorded at several chimpanzee study sites: Budongo Forest in Uganda (Sugiyama, 1968), Gombe National Park in Tanzania (van Lawick-Goodall, 1968), and the Kasakati-Mahali area in Tanzania (Nishida, 1973). Numerous field experiments conducted in Guinea and Zaire, in which chimpanzees were exposed to mechanized leopard dummies and other unfamiliar items, have also yielded valuable information on their potential for technological behavior, and especially in the use of objects as weapons (Albrecht & Dunnett, 1971; Kortlandt, 1963, 1965, 1967, 1968; Zon & Orshoven, 1967). Similar 'attack' responses have, however, not yet been observed in interactions between chimpanzees and live carnivores, including leopards (Teleki, 1973a). Moreover, similar tests in which Kortlandt exposed baboons in Uganda to a mechanized leopard elicited frenzied attacks but not weapon-use (Eimerl & DeVore, 1965; Kortlandt, pers. comm.).

This catalogue of baboon and chimpanzee technical skills shows that the frequency and distribution of such performances differ remarkably in these particular cercopithecoid and pongid genera. Reports of chimpanzee field research throughout Africa are laden with incidents of technological behavior, whereas reports of baboon field research contain only sparse cases at a very limited number of sites. The discrepancy observable in the technical capabilities of baboons and chimpanzees is reminiscent, even though both are collector-predators, of the discrepancy in the capabilities of chimpanzee collector-predators and human gatherer-hunters.

3. Chimpanzee Subsistence Technology

The technical skills of chimpanzees are highly diversified even within the special context of subsistence, and their technological repertoire seems to contain some flexibility within as well as between populations.

(a) *Skills exhibited and materials utilized*

The technical skills and materials used in naturalistic food-getting activities are shown in Table 1. When summarized, these include: *pounding* of hard items, such as nuts and hard-shelled fruits, with sticks and stones; *probing* for honey and insects, usually ants or termites, with twigs, vines, grass stalks and bark strips; *prying* open the nests of arboreal

Table 1 Vital data on chimpanzee subsistence technology

Country	Site	Map no.	Food type	Manipulation	Objects used	Modification	References
(West Africa)							
Liberia	?	1?	nuts	pounding	stones	none(?)	Savage & Wyman (1843-44)
Ivory Coast	?	2	palm nuts	pounding	stones	none noted	Beatty (1951)
	T'ai Forest Reserve	3	hard-shelled fruits	pounding	sticks and stones	none noted	Rahm (1971), Struhsaker & Hunkeler (1971)
Cameroon	regional survey	4	termites	probing	sticks (twigs)	chewed and worked smooth	Struhsaker & Hunkeler (1971)
Rio Muni	Dipikar Island	5	termites	probing	sticks, twigs	breaking to suitable length, stripping of leaves and other projections	Jones & Sabater Pi (1969)
Rio Muni	near Ayimken	5	termites	probing	sticks, twigs	breaking to suitable length, stripping of leaves and other projections	Jones & Sabater Pi (1969)
Rio Muni	Mt Okoro Biko	6	termites	probing	sticks, twigs	breaking to suitable length, stripping of leaves and other projections	Jones & Sabater Pi (1969)
Zaire	?	7?	honey	probing	twigs	?	Merfield & Miller (1956)
Tanzania	Gombe National Park	8	ants	probing	sticks, twigs vines, grasses	breaking and biting to suitable length, stripping leaves and other projections	van Lawick-Goodall (1968, 1970)
			ants	prying (var. on probing or digging)	sticks, twigs	breaking to suitable length	van Lawick-Goodall (1970), Teleki (pers. observ.)

		ants	digging	sticks	breaking to suitable length	van Lawick-Goodall (1970), Teleki (pers. observ.)
		termites	probing	twigs, vines grasses	breaking to suitable length, stripping of leaves and other projections	van Lawick-Goodall (1968, 1970), Teleki (pers. observ.)
		honey brain tissue	probing sponging	sticks, twigs leaves	none noted chewed into an absorbent mass	van Lawick-Goodall (1970) Teleki (1973 <i>b</i>)
		water	sponging	leaves	chewed into an absorbent mass	van Lawick-Goodall (1968, 1970)
Tanzania	Kasakati Basin	ants	probing	twigs, bark strips	breaking to suitable length	Suzuki (1966, 1969)
		termites	probing	twigs, bark strips	breaking to suitable length, stripping of leaves and other projections	Suzuki (1969)
Tanzania	Makolongo & Kabogo Pt	honey termites	probing probing	twigs twigs, vines	none noted none noted	Izawa & Itani (1966) Izawa & Itani (1966)
Tanzania	Mahali Mtns	ants	probing	sticks, twigs vines, bark strips	breaking and biting to suitable length, stripping of leaves and projections	Nishida (1973)
		ants	prying (var. on probing or digging) wiping (var. on sponging)	sticks	none noted	Nishida (1973)
		ants		leaves	crumpled by hand into wad	Nishida (1973)

ants with sticks; *poking* at unfamiliar items, including foods, with sticks or grasses used as 'olfactory aids'; *digging* into the terrestrial nests of safari ants with sticks; *sponging* water from hollows in trees, and brain tissue from a skull cavity, with wads of leaves crumpled by chewing; and *wiping* up ants with leaves crumpled by hand.

An interesting footnote to the above list is the fact that chimpanzees have not yet been observed to use objects for killing or dismembering prey, even though 183 cases of predation have been recorded since 1960 (Teleki, in press). The absence of a link between technical skills and predatory habits among chimpanzees is on the one hand similar to other kinds of limitations observable in the application of technical skills to subsistence among baboons; but on the other it serves to emphasize a rift between chimpanzee and human subsistence technology by virtue of the fact that the latter hunt almost exclusively with the aid of technological devices.

Although the above examples of technological behavior involve several types of foods and objects, the actions performed are themselves limited in variety. If prying, poking and wiping are regarded as variations on the respective themes of digging, probing and sponging, then only *pounding*, *probing*, *digging* and *sponging* remain as distinct technical skills. Digging with sticks, which is a standard technique among human gatherer-hunters, is not entirely absent from this repertoire; but it occurs rarely, having been seen only during the opening of ant nests with sticks. It is noteworthy, however, that an activity which is somewhat analogous to digging—namely, probing for insects—is widely and frequently performed by chimpanzees. But the tubers and other subsurface flora which comprise the staple resources of some gatherer-hunter populations cannot be exploited by these omnivorous apes. Herein lies another limitation highlighting the difference between chimpanzee and human subsistence technology.

The manipulation of objects in contexts other than subsistence is rarely accompanied by actions of modification, so it is doubly significant that many of the food-getting technical skills exhibited by chimpanzees include a component of preparatory modification. The form of an object is most commonly modified when materials are prepared for probing and sponging: twigs and vines are stripped of leaves and other projections; sticks, twigs, vines and grasses are broken or bitten off to suitable lengths; and leaves are chewed or manually crumpled into absorbent masses. These observations suggest that there may be, and may well have been, a stronger linkage between modification and subsistence activities than between modification and other patterns of technological behavior, such as aggressive use of objects.

Chimpanzees sometimes carry objects about for periods of more than an hour and for distances greater than a kilometer. Such transport behavior occurs mainly in connection with termite collecting, when an appropriate probe may be carried from mound to mound as an individual seeks new tunnels. Materials such as vines and grass stems are usually carried in the hands or between the lips. The context of insect-collecting provides the only definite cases where transportation is an intermediate activity between a series of applications. But there are other situations in which transportation is an anticipatory activity, as when a chimpanzee sets off to probe for termites and then selects and prepares an appropriate vine or grass stalk some 100 or more meters before arriving at a mound. And in still other situations chimpanzees will leave one place to fetch an object from another: e.g. when getting a new probe during a 'fishing' session, or when getting an object to strike or throw at an antagonist. The apparent absence of transport behavior in baboons, the conditional presence of rudimentary transport behavior in chimpanzees,

and the routine practice of long-distance transport behavior in humans are suggestive of ordered levels of complexity in Primate subsistence technology.

Surveys of Primate technical skills show that objects are most commonly and widely used in agonistic situations (e.g. Hall, 1963). This behavioral context may, in effect, have been the Primary stimulus, or original source, for developing technical skills. However, even if the manipulation of objects was initially associated with agonistic behavior, as proposed by Kortlandt & Kooij (1963), the modification and transportation of objects probably emerged in conjunction with subsistence activities. Whereas sticks need not be modified for use as clubs, twigs must usually be modified for use as probes. Similarly, whereas manipulative skills probably appeared in the very early stages of Primate evolution, modification and transportation skills may not have appeared until the emergence of pongids. More subtle refinements in technology, such as a shift from the use of sticks to expose insect nests to the use of sticks to dig for subsurface flora, may only have appeared much later, perhaps with the emergence of the earliest hominids. An evolutionary model of technological development would, in this case, have involved a feedback system wherein modification and probably long-distance transportation were applied to weapon making long after these activities became functional in a collecting or gathering subsistence context.

(b) Geographical and individual variability

The most intensive studies of chimpanzee behavior and ecology have been conducted in eastern Africa, but evidence of technological behavior has recently been discovered in other parts of the continent. The known geographical distribution of chimpanzee subsistence technology is shown in Figure 1, which supplements the data listed in Table 1. The repertoire of skills performed in Gombe National Park and in the Kasakati-Mahali area (including Kasakati Basin, Makolongo, Kabogo Point, Mahali Mtns) is probably close to being fully documented. But information from other regions, and notably from populations at the westernmost portion of the *Pan* range, is likely to be rather incomplete. For example, most of the pounding data from Liberia and Ivory Coast, and the probing data from Cameroon and Rio Muni, derive from the material remains of these activities.

Figure 1. Geographical distribution of chimpanzee technological complexes.



Hence, an assessment of any geographical variability that may occur in technological traits rests on much firmer ground at the eastern than at the western extremes of the continent. Long-term studies in western and central Africa are sorely needed; until such have been conducted, the following regional comparisons remain highly tentative, being more an instructive exercise than a final statement of fact.

The close similarities observed in the technical skills exhibited at adjacent sites, such as those in Tanzania or in Cameroon and Rio Muni, attests to the behavioral integrity of what probably were, until quite recently, larger population units. Based on this assumption, the two neighboring sites in Liberia and Ivory Coast (2 and 3 on map), the three intermediate sites in Cameroon and Rio Muni (4, 5 and 6), and the two adjacent sites in Tanzania (8 and 9) can be treated as three discrete units labeled as populations A, B and C, respectively.

Table 1 showed that pounding is associated with hard fruits and nuts, probing with insects and honey, digging with ants, and sponging with water and brain tissue. These all appear to be highly functional relationships in which the actions performed and the materials utilized are closely tied to the types and locations of the resources being exploited. These functional relationships define *technological complexes* which consist of specific linkages in patterned actions, in materials and in foods (e.g. pounding on nuts with stones), and these complexes in turn combine to form the *technological repertoire* of a given population. The patterned actions may themselves be composed of behavioral sequences, such as scanning, locating, selecting, picking up, shaping and utilizing, all of which are preliminary to food consumption. Furthermore, each complex contains little or no variability from region to region—that is, the pattern of probing for termites is similarly performed wherever the complex appears—but the matrix of complexes which comprises a full repertoire may show considerable variability from one region to another.

The full complement of technical skills—pounding, probing, digging and sponging—has not been documented at any single study site, nor in any one of the three labeled populations. Pounding is currently known only in population A. Despite 19 months of field surveying in the Cameroon area of population B, Struhsaker found no evidence of this trait (Struhsaker & Hunkeler, 1971); similarly, 20 months of chimpanzee surveys in the Rio Muni area of population B yielded no signs of pounding (Jones & Sabater Pi, 1971). In population C, hard-shelled fruits are opened simply by hitting the items themselves against hard surfaces, such as rocks or tree trunks (Izawa & Itani, 1966; van Lawick-Goodall, 1968). The pounding technique, in which one object is used to hit another, thus seems to be restricted to regions west of a zone that is approximately delineated by 5°E longitude.

Probing for insects and honey has been extensively recorded in the regions inhabited by populations B and C, and this is the most widespread complex known today. Some intrapopulation variability may occur in this complex: both populations B and C probe for termites whereas only population C is known to probe for ants; and members of population B seem to favor sticks and twigs while members of population C seem to prefer grass stalks, vines and bark strips. In broad terms, the zone marked by the 5°E longitude line serves as the approximate western limit for the probing technique, as no evidence of this complex has been obtained in population A (Struhsaker & Hunkeler, 1971).

Sponging up water and brain tissue, or wiping up ants, is known at present only in population C. Although the sponging complex may be a regional variation on the same scale as the pounding complex, there is some possibility that this technical skill has not

yet been observed outside Tanzania simply because of differences in the scope of field studies conducted elsewhere. The distribution of digging, which has also been observed only in Tanzania, may be similarly biased. However, when the facts are taken as they now stand, pounding is restricted to population A, sponging and digging to population C, and probing to populations B and C. The longitudinal lines of 5°E and 25°E serve as rough boundaries for the technological repertoires. It is perhaps noteworthy that the 29°E meridian, which separates the main basins of central and western Africa from the rift zone of eastern Africa, has been cited as a rough boundary for baboon and chimpanzee predation on mammals, a phenomenon which occurs at several sites east of this line (Kortlandt & Kooij, 1963; Teleki, in press).

Not even the most widely exhibited technical skill, probing for insects, has been recorded at some sites lying well within the range of this complex. In Uganda, for example, where investigators have intermittently studied chimpanzees since 1962 (Reynolds & Reynolds, 1965; Sugiyama, 1968, 1969), all forms of subsistence technology seem to be absent. Such negative evidence is at best dubiously reliable, but the apparent absence of certain complexes in local populations does introduce the issue of technological variability within a regional population.

There is some evidence to indicate that the patterns of technological variation outlined above are less a function of opportunistic than of behavioral variability. Although termites are known to occur from the westernmost to the easternmost chimpanzee habitats where some sort of subsistence technology is practiced, these insects are not everywhere exploited via the probing technique. Similarly, the nuts of oil palm trees are apparently consumed by chimpanzees throughout Africa, yet the pounding technique has been observed only in the westernmost region. These same nuts are a favored food of population C as well, but the latter simply strip away the external pulp with their teeth and sometimes swallow the nuts whole. If further field studies show that technological complexes do vary within or between populations despite uniformly available food resources, an element of cultural heritage may play a part in the transmission of skills.

The acquisition and propagation of a technical skill, such as probing for termites, is known to involve learning processes which are in turn probably affected by individual differences in ability. Chimpanzee infants learn their 'fishing' skills by watching older individuals and then practicing the technique for several years (van Lawick-Goodall, 1968, 1970), and the level of sophistication achieved by the time adulthood is reached is not necessarily uniform in all members of the community, or social unit. These individual differences may lead to considerable variability in the performance of any given technical skill. Thus, the transmission of such a tradition might be dependent upon both the sophistication of the performants and the aptitude of the learners.

Such individual variability is in fact observable in many contexts other than that of subsistence technology. Some members of a chimpanzee community participate regularly in predatory episodes whereas others may avoid these situations entirely (Teleki, 1973*b*); some members of a group may consistently use objects in attacking a mechanized leopard whereas others exhibit no such technical skills (Kortlandt, pers. comm.). The examples are many and diverse, individual variability being a pervasive theme in most of the activities performed by chimpanzees wherever they have been studied in depth. Technological behavior may, therefore, be but one of many activities that are differentially performed within a single population and perhaps even within a single social unit.

The mechanisms whereby chimpanzee technological repertoires differentiate through time remain obscure largely because the data are still so incomplete. Models of behavioral variability in subsistence habits must therefore be sought elsewhere. Intensive studies of certain Japanese macaque populations, in which kin, consort and other social ties regulate transmission of such spontaneously acquired subsistence techniques as potato-washing and wheat-sifting (e.g. Azuma, 1973), provide one potential model. The similar social mechanisms which have been tentatively identified as regulators of chimpanzee predatory behavior (Teleki, 1973*b*) constitute another potential model. In both of these situations, not all members of a social unit learn and apply the various subsistence techniques uniformly and unilaterally. Depending on the extent of inter-unit migration, such variability could enhance or inhibit transmission of a given behavior within and/or between populations.

Most Primates can be classed as omnivores, but the degree to which any one population or social unit is omnivorous can vary tremendously. Baboon and chimpanzee populations, for example, exhibit great variability in predatory frequency, perhaps because this behavior is affected by both social and environmental contingencies (Teleki, *in press*). So the mechanisms regulating a subsistence activity, such as predatory behavior, and any other activity associated with subsistence, such as technological behavior, may set the stage for differential development of skills. Physical and/or psychological limitations on acquiring and transmitting technical skills may, on the other hand, offset this variability in such a way that an upper limit to technological achievement is met at some point. The balance between exploitative skills and available resources would, in effect, tend to remain at equilibrium at a given place and over a short period of time. Consequently, the Gilgil baboons (e.g. Harding, 1973) can no more be expected to exhibit the kinds of technical skills (and predatory habits) possessed by the Gombe chimpanzees (e.g. Teleki, 1973*c*) than can the latter be expected to exhibit the kinds of technical skills (and hunting habits) possessed by the Kalahari bushmen (e.g. Silberbauer, 1972), even though all three populations are fully omnivorous.

4. Chimpanzee Termiting Skills: A Personal Inquiry

The techniques used to probe into termite mounds and ant nests have been closely studied at the Gombe and Mahali sites (van Lawick-Goodall, 1968, 1970; Nishida, 1973). My purpose here is to supplement these descriptions with comments on the expertise needed by chimpanzees to perform this task successfully.

During the course of two termite-collecting seasons, in 1968 and 1970, I followed Gombe chimpanzees on their rounds of termite mounds with the intention of learning about the following problems. (1) How does a chimpanzee find the entrances to termite tunnels which, during the diurnal foraging period of these apes, are covered by an homogeneous layer of clay? (2) How does a chimpanzee select the object to be used in probing for termites, and what are the essential properties which enable the selected object to function suitably? And (3) what actions must be executed in order to ensure a rewarding catch of termites? Early in my observation I had become impressed by the ease and facility with which adult chimpanzees performed the probing technique, and my queries were prompted by a suspicion that the existing descriptions of this technological complex, which seemed to focus mainly on the mechanical actions involved, did

Plate 1. Adult male chimpanzee (Faben) carefully draws a length of grass from a termite tunnel with his left hand and begins to extend his lower lip in preparation to pulling the soldier termites off the 'fishing' tool.



Plate 4.(a) Juvenile male chimpanzee (Sniff) twirls a branch about with both feet in solitary play, also exhibiting a moderately intense play face. (b) Adult female chimpanzee (Flo, upper left) intently grooms a handful of leaves while two of her offspring (Flint, left foreground; Fifi, upper right) watch the lip and finger movements closely. Such 'object-grooming' often serves to elicit social grooming from those who watched the performer.



not adequately convey what chimpanzees must know in order to 'fish' skillfully for these insects. In particular, I wished to discover something about the psychological prerequisites involved.

One old and seemingly highly skilled individual, Leakey, was followed most consistently during the second season—at which time I was conducting a study of ranging habits, daily regimen and community structure—because it seemed evident by then that patterned ranging habits, with regular versus random visits to certain mounds, might play an important part in the development of an individual's efficiency and competence. Moreover, I frequently endeavored to imitate the techniques under observation, while alone or when in the company of Leakey, so as to gain personal experience in the skills so routinely executed by this individual. (All aspects of the procedure, including the final tasting of the insects, were practised.) As described below, these experiences revealed new information about the physical and psychological factors involved in this subsistence activity, which insight eventually led to the suspicion that anthropologists tend to underestimate pongid technical skills when defining the 'uniqueness' of man.

(a) *Setting the stage*

As reported by van Lawick-Goodall (1968, 1970), termite-probing, or 'fishing', consists of the following basic actions: scraping away a thin soil layer that covers the entrance of a tunnel, using a finger or thumb; carefully poking an object into the exposed tunnel mouth; pausing momentarily while holding the protruding end of the object in one hand; extracting the object with its attached soldier and worker termites; and picking off the desired termites (soldiers being preferred) with the lips and teeth while holding the probe in one hand and stabilizing the free end on the other wrist. Nearly all members of the Gombe study population (*ca.* 50 individuals) devote at least 1–2 hr and sometimes 4–5 hr daily to this one subsistence activity when termites are in season. Individuals of all but the youngest age classes exhibit the probing skills, although adults tend to show the greatest persistence and proficiency.

Termite-probing is an annual but not an everyday activity, as the 'fishing' season only lasts about 2 months per year, the most productive period being closely linked to the onset of rainfall in October or November. This climatic shift also regulates the termite reproductive and migratory cycles, with mass migration occurring about 2–3 weeks after the rains begin. There is some evidence that chimpanzees anticipate these seasons, perhaps via climatic cues, as they sometimes begin to examine mounds prior to the first rains. Out-of-season termiting bouts do occur occasionally, but the probing technique is rarely practiced during the height of the dry or rainy seasons. It is also relevant that tunnels must daily be relocated and opened even during the most intense collection period, for termites at Gombe are essentially nocturnal (except during the migration time) and regularly block all entrances to their mounds. Chimpanzees sometimes suck on soil from these mounds, presumably because it contains salt, a mineral which they actively seek in other circumstances as well.

(b) *Locating tunnels*

Having repeatedly observed individuals approach a mound, make a rapid visual scan of the surface while standing on or beside it, and reach decisively out—with a high degree of predictive accuracy—to uncover a tunnel, I was soon impressed by the apparent

ease with which tunnels could be located. In attempting to learn the technique, I applied several experimental procedures: examining in minute detail all crack patterns, protuberances, depressions and other "topographic" features in the clay. But, after weeks of futile searching for the essential clue, I had to resort to scraping mound surfaces with a jackknife until a tunnel was inadvertently exposed. My inability to find any physical features which could serve as visual cues eventually led me to realize that chimpanzees may possess knowledge far beyond my expectations.

Consistent following of chimpanzees during the two termiting seasons, and especially among the mounds scattered throughout lower Kakombe Valley (see Teleki, 1973*b*, for maps of the study area), revealed that some individuals routinely visit certain sets of mounds, often travelling along a prescribed network of trails from one to another in the sequence. Thus, each chimpanzee seemed to exploit a *core set* of mounds most heavily, although other mounds encountered during more extensive forays are of course utilized on an opportunistic basis. Presumably the mounds in the core set, which may vary in number from about 10 to 25 per individual, are more familiar to a given individual than are the mounds less regularly visited. Some or all of the core mounds may be visited on a daily basis during the collecting season, but the regularity of visits may be influenced by other behavioral opportunities (e.g. an estrous female) which may be present at the time. Many of the mounds within a core set may be shared by several individuals, so the 'termiting ranges' may overlap extensively. Because only 1-3 chimpanzees are likely to work a mound simultaneously, competition occurs only rarely. There is some indication, however, that adult females, and particularly mothers, who tend to have much smaller ranges than other adult classes, exhibit an unusual degree of competition for this resource (Baldwin, pers. comm.).

A chimpanzee's presumed familiarity with a core set of mounds provides the main clue to the problem of locating tunnels. The only hypothesis which, at this point, seems to reasonably account for the observed facts is that an adult chimpanzee may know (memorize?) the precise location of 100 or more tunnels in the most familiar mounds. Moreover, since intensive probing is restricted to a short annual season, the possibility that chimpanzees retain a mental map of core mound features during the intervening 10 months must also be considered. That chimpanzees require a prolonged learning period (i.e. 4-5 years) to gain proficiency in this technique (van Lawick-Goodall, 1970), and that some individuals are known to have the capability to retain specific information for many years, provides circumstantial support for this hypothesis. However, only a detailed study of termite-collecting habits, and of termite behavior, is likely to resolve the following kinds of questions. Is the error rate in locating tunnels higher at mounds that are less familiar than those in a core set? Are the tunnels used by a given individual in a core set of mounds consistently the same for long periods of time? Is there a period of greater error in locating tunnels at the start of each season?

(c) *Selecting materials*

An examination of the skills needed for selecting an object having the requisite properties for successful probing was the next step in the investigation. When performed by experienced chimpanzees, the selection procedure seems deceptively simple. After a brief visual scan of the nearby vegetation, a chimpanzee will usually extend a hand and deftly tear off a twig, vine or grass stalk. Sometimes the individual must move a few paces away

from the mound and fetch a suitable probe, and in some cases 2–3 objects are initially selected. These may be rapidly examined and discarded until some specification is met in one, or several may be carried to the mound for subsequent selection. Whenever it occurs, the selection is made in a swift, almost casual manner, and modification is begun if necessary. Without being aware of the nuances involved, it is easy to undervalue the proficiency needed to perform these manouvers.

Chimpanzees presumably have the experience whereby the properties of an object can be evaluated before it is applied to the task of probing, for the rate of error in selecting probes is not high. For the novice human observer, however, the utilization phase of the sequence holds the key to selection because the appropriateness of an object becomes apparent only through the trial-and-error of application. It is not difficult to find a grass stalk or vine stem of suitable dimensions, nor is it difficult to trim away leaves and other projections before breaking or biting it down to the required length. These are routine motor patterns which entail some dexterity but little prior experience. But there are other physical properties which must precisely fit the intended task, and these are less easy to anticipate. When probing for termites, the specifications are in fact surprisingly stringent: if the vine or grass selected is too pliant, it will buckle and collapse (accordion-like) when inserted into a twisting tunnel; if, on the other hand, the object is too stiff or brittle, it will catch on the tunnel walls and either break or resist entry to the necessary depth. An intermediate range of qualities must therefore be selected if probing is to yield many termites.

Despite months of observing and aping adult chimpanzees as they selected probes with enviable ease, speed and accuracy, I was unable to achieve their level of competence. Similar ineptness can only be observed in chimpanzees below the age of about 4–5 years. My experiences suggest that selection proficiency is a learned skill which must, like tunnel-locating, entail a considerable amount of trial-and-error behavior backed by long-term retention of the results. The retention span may actually cover the lifetime of an individual.

Behind these refinements is the fact that the materials used in collecting termites and ants from terrestrial nests differ considerably in their properties, due in large part to the nature of the resources being exploited. At Gombe, termite mounds (*Macrotermes bellicosus*) are covered by a uniform clay layer which is extremely hard when dry, whereas ant nests (*Anomma nigricans*) consist of loosely aggregated soil particles which can easily be pushed away by hand or stirred up with a stick. The objects commonly selected for collecting ants are large, stiff sticks or branches which can be forcefully shoved, end foremost, into the nest without bending or breaking. The dimensions and properties of these objects are thus quite different from materials used in probing, where the combined criteria of pliability and tensile strength are more important. To complicate the issue further, the techniques and materials used to collect ants from arboreal nests (*Crematogaster* spp. and *Camponotus* spp.), as described by van Lawick-Goodall (1968) and Nishida (1973), resemble those used in collecting termites from terrestrial mounds. Exploitation of each food resource therefore entails selection procedures geared to a specific task and resource. Given the possibility that technological repertoires differ from region to region, each stage of a particular complex may well have to be learned via a cultural tradition that is passed from individual to individual within a given population, one of the most direct and stable routes of learning being the prolonged associations between mothers and their offspring.

(d) Utilizing probes

Having failed to meet chimpanzee standards of aptitude and skill in the preceding stages of termite-probing, I nonetheless set out to acquire some competence in the 'fishing' stage, which seemed relatively simple in comparison to locating tunnels and selecting probes. Consequently, I spent many hours inserting probes, pausing for the designated interval, and pulling them out again—without getting any termites. Only after some weeks of nearly total failure—an uncommonly brief learning span, at least for this particular panthropologist—did I finally begin to grasp the problems involved. Although a very rich tunnel may initially produce moderate rewards even if skill is essentially lacking, a newly opened tunnel (in which termites are perhaps still too far underground) or a partly 'fished-out' tunnel (which termites may block off at some subsurface level) requires the application of subtle techniques. Skill is particularly necessary if the period of successful probing is to last more than a few minutes.

In order to collect these subterranean termites, the probing object must first be carefully and dextrously inserted to a depth of about 8–16 cm, with appropriate turns of the wrist so that the object navigates the twisting channel. The probe must then be gently vibrated with the fingers during the prescribed pause, for without this movement the termites may not be stimulated into biting firmly onto the probe. However, if the vibration is performed too lengthily or roughly, there is an excellent chance that the probe will be cut through by the mandibles while still in the tunnel. When these preliminary actions have been correctly performed, the probe, presumably with dozens of termites now attached, must be extracted from the tunnel. Once again there are nuances to be observed. If the object is too rapidly or clumsily pulled out, the insects are likely to be scraped off along the sides of the tunnel, which then yields nothing but a shredded probe. The hand motions must be reasonably but not overly swift and, once started, uniformly fluid and graceful. If the tunnel is particularly tortuous (a feature which can be determined during insertion of the probe), the success of the catch can be ensured by a slow twisting of the wrist while the probe is pulled out.

(e) Considering the results

These, then, are the sequential behavioral components of a chimpanzee technical skill which, when viewed superficially, seems to be a far simpler task than those routinely performed by human gatherer-hunters. But my participant observation at Gombe unveiled the remarkable amount of experience and finesse needed by a chimpanzee to perform this subsistence activity. When such qualitative aspects of subsistence technology are omitted from descriptions, the risk of dispensing with such skills as 'rudimentary' increases. Incompetent as they were, my attempts to acquire the skills of locating tunnels, selecting materials, inserting probes, and extracting termites left me with a healthy measure of respect for chimpanzee technical ability, as well as with a nagging suspicion that the physical and psychological capabilities needed to develop, apply and transmit such skills may differ in degree but not in kind from those needed by humans to locate, expose and gather insects and subsurface flora. In other words, a question about how an integrated sequence of technological behavior, where the omission of any single stage results in failure, was initiated, put together and finally fixed into the repertoire of a population, can now be directed at nonhuman as well as human Primates.

If these tentative conclusions are confirmed by further field research, the technological gap postulated to exist between the nonhuman and human Primates would be partly though not entirely filled. The key word here is 'partly', for it remains clear that the full scope of subsistence technology probably differs considerably, in terms of both the range and the refinement of skills, from one Primate genus to another: human gatherer-hunters are unquestionably more dependent on a wider array of technical skills and materials than are nonhuman collector-predators.

5. Termiting Skills: Interspecific Comparisons

The simplest way to illustrate such differences in degree is by reviewing some comparative data on the termiting techniques exhibited by baboons, chimpanzees and humans in Africa. This sample of Primate populations—ranging from a cercopithecoid through a pongid to a hominid—serves to mirror the increasingly complex technological capabilities, as well as the levels at which limitations arise, that can be observed in the behavior of primates having different phylogenetic histories.

(a) *Baboon and chimpanzee techniques*

General differences in the technological behavior of baboons and chimpanzees have already been summarized. The purpose here is to highlight specific differences in the termite-collecting skills of these Primates. The baboons and chimpanzees of Gombe National Park, whose insect-eating habits have been described by Ransom (1971) and Lawick-Goodall (1968), provide a uniquely simple opportunity to focus on modes of exploiting a single food resource in a single habitat.

For the Gombe baboons, the termiting season is almost exclusively limited to the 2–3 weeks during which migrations occur. Thus, their bulk intake consists of winged termites that are collected, singly or in clusters, as they emerge, mass and fly away from open tunnels. Crawling and flying insects are collected with hands and/or lips, and baboons can sometimes be seen leaping up and down on mounds in an effort to grab termites in flight. (These methods are also used by other Gombe Primates, such as the 'leaf-eating' colobus and the blue monkey.) Several baboons may work a mound simultaneously, but rarely do two or more collect at a single tunnel mouth. Baboons are sometimes displaced from mounds by arriving chimpanzees, especially by adult males, and may then sit and watch the apes collect insects. But observers have not seen baboons using an object as a probe, even when these have been discarded on a mound or abandoned in a tunnel by the chimpanzees.

The Gombe chimpanzees also collect some winged termites during the migration period, yet they will in many cases ignore the insects massing at tunnel entrances and instead probe for soldiers elsewhere on the same mound. Probing is clearly the standard chimpanzee technique. As a result, the termite-collecting season is extended by several additional weeks before and after the short migration period, and the bulk intake consists of soldier termites. The technical skills developed by chimpanzees have clearly affected exploitation of this food resource, and the exploitative potentials of the two genera now differ markedly in duration if not in bulk. And, although both primates show a great fancy for termites, their respective preferences and methods largely obviate competition for a limited-supply resource.

The value of the Gombe example lies in its exposure of what appear to be fixed patterns of behavior in baboons and to some extent in chimpanzees. What, in other words, inhibits baboons from adopting, at least to a limited degree, the techniques used by chimpanzees? And what kinds of psychological phenomena are involved in this limitation? The questions become doubly intriguing when set against a larger regional background, for this apparent limitation is not necessarily characteristic of the genus *Papio*. According to the incidental reports collected by Kortlandt & Kooij (1963), some baboons do use pieces of wood to widen the entrances of termite nests. Whether this is a regional difference in behavior comparable to those documented for chimpanzee populations A, B and C remains unknown, as does the problem of whether the more technically skilled baboons exhibit similar levels of sophistication and persistence as do chimpanzees. Further field studies are much needed to elucidate such problems.

Given the general differences between baboon and chimpanzee technological repertoires, as well as the specific discrepancies observed in termite-collecting at Gombe, it is currently tempting to postulate that the technical skills in these genera are related to varying levels of cortical complexity, and hence to differential learning and performing capacities. If so, a model of behavioral evolution might be integrated with the numerous existing models of biological evolution. But there are crucial, as yet unresolved issues: for example, to what extent are such technological limitations characteristic of species or genera, and how are the limitations adaptively significant?

(b) *Chimpanzee and human techniques*

In a survey of human insect-eating habits, Bodenheimer (1951) shows that termites, ants and other insects are highly favored by numerous human populations, many of which live in regions also inhabited by baboons and/or chimpanzees. Taking Africa in its entirety, human techniques of termite-gathering are extremely variable and often much more efficient than those of termite-collecting baboons and chimpanzees; on a local level, however, some of the human techniques are the same as those used by nonhuman Primates.

In western Zaire, for example, members of the Baluba tribe insert palm leaves into termite tunnels, pause to stir the protruding probes, and finally withdraw the probes laden with clinging soldier termites. Elsewhere in western Zaire, large poles are driven into termite mounds to make holes about a meter in depth; the poles are withdrawn, and small "brooms" made of grass are inserted into these holes; a noise is then made with the tongue so as to imitate the sound of raindrops falling on the clay, and the probes are turned slightly by hand so that termites will clamp onto the grass; then the probes are withdrawn, and the soldier termites are eaten one-by-one immediately, or they may be collected in baskets and taken away. A variation on the theme of imitating raindrops occurs in northern Zaire, where two pieces of wood are beaten against the mound surface. A rather common form of suberfuge, stick-beating has also been observed at Mt Elgon, on the Uganda-Kenya border, and other areas. The soil of termite mounds is in some places also eaten, the claim being that such soil contains higher concentrations of salt.

At Gombe, where termites are also actively sought by the indigenous human population, individuals or small groups frequently go termite-gathering during the rainy season. The insects are often gathered at dusk, the following technique being commonly used: a kerosene lantern is placed on or near the mound, both to aid vision and to act as

a beacon for the insects; a large portion of the mound surface is scraped away with a panga (machette) blade to expose and stir up the insects; the exposed milling mass of termites is picked or scooped up into a dish or basket by hand and sometimes by leaves or fronds. During the 2-3 week migration season mainly winged termites are gathered, but both soldiers and workers are taken during the rest of the rainy season. On one occasion I observed a man rapping on a mound with two small sticks, presumably in order to imitate raindrops. Thus, three ways of exploiting a given resource, two of which involve technological behavior, can be compared at this one site. The human technique further extends the duration of the termite-gathering season, much beyond the periods in which baboons and even chimpanzees can collect these insects, and perhaps increases the annual yield as well. The baboon, chimpanzee and human populations in Gombe National Park clearly exhibit a series of increasingly sophisticated technical skills which reflect distinct, perhaps species-specific, levels of technological (and psychological?) capabilities.

After emphasizing the remarkable degree of similarity which occurs in some chimpanzee and human termiting techniques, it should also be stressed that the above comparisons are not fully representative of the rich array of skills performed by various human populations. Whereas chimpanzees throughout much of Africa possess a single technological complex for termite-collecting, human populations exhibit extensive regional variability in techniques which can include fumigating, digging, pouring water onto mounds, placing upturned dishes onto sticks driven vertically into the clay, and so on. Moreover, only humans are known to practice the subtle subterfuge of imitating raindrops so as to entice termites to the surface. This one skill may alone extend the gathering season by weeks or months.

These anecdotal cases do not provide a comprehensive picture of Primate technical skills. Numerous gaps must be filled in with further comparative field work. But the examples do suggest that subsistence activities, and to some extent even technical skills, can be arranged as overlapping segments on a behavioral continuum. When such continuities can be documented among extant cercopithecoid, pongid and hominid populations, the resultant behavioral models can be used to supplement morphological trends in primate evolution and also to lay a foundation for reconstructing the probable subsistence habits of the earliest hominids. Although attention has focused here on technological behavior, this approach can be adopted with other subsistence activities, such as predatory and hunting behavior (Teleki, in press).

6. Conclusion and Discussion

The application of technical skills to subsistence activities, and particularly to hunting game, has been widely cited as a characteristically human condition. The material remains of technological behavior, such as shaped artefacts, are often regarded by prehistorians as a sign of human culture, and have thus been ranked as a prime ingredient in the process of hominization (e.g. Oakley, 1959). This conceptual trend was readily adopted in other branches of the discipline, and notably by those cultural anthropologists who were interested in separating nonhuman primate society and primitive human culture (e.g. Sahlins, 1959). Now deeply ingrained in our minds and our texts, the trend continues to be propagated in these circles (e.g. Fried, 1967) despite the many advances which have begun to sway members of other subdisciplines toward an alternative position (e.g. Lancaster, 1968; Mann, 1972). Needless to say, the impact of separatism upon

anthropological theories of human evolution has been immense, for the above is by no means an isolated case history. Many traits other than technology—among which can be numbered predatory behavior, nuclear family structure, division of labor by sex, kinship relationships and lineage ties, incest prohibitions, sharing and cooperation—have been routinely linked to the divergence of a savanna-dwelling, meat-hunting hominid from a forest-dwelling, plant-collecting Primate heritage. That this determination to regard humans as behaviorally and psychologically supreme (an attitude which retains a strong flavor of “special creation”) contrasts with a readiness to accept biological affinities (an attitude which often leads to scientific destruction in the name of human welfare) does not seem to have caused excessive consternation among students of human behavior and evolution.

Yet it steadily becomes more obvious, as evidence accumulates about what Primates actually do in their native habitats, that nearly all of these ‘human’ traits can be identified among the nonhuman Primates. Chimpanzees are in fact rapidly becoming the prime exception to the separatist perspective, as *Pan* is already known to exhibit more such traits than any extant genus other than *Homo* itself. Chimpanzees are, for example, known to cooperate in prey pursuit, to practice division of labor in pursuing and capturing prey, to share meat along lines reflecting kinship, consort and other social ties—all within the single context of predation (Teleki, 1973*b,c*). And, as shown in this report, chimpanzees are also technically skilled Primates which, as Lancaster (1968) has aptly pointed out, makes this living pongid the best candidate for mirroring the ancestor postulated for the origin of the hominid line. Similar advances continue to occur along many avenues of investigation, some of the most outstanding being family structure (van Lawick-Goodall, 1968, in prep.), community organization (e.g. Itani & Suzuki, 1967) and communication (e.g. Gardner & Gardner, 1969; Rumbaugh, Gill & von Glaserfeld, 1973).

Once *Homo erectus* sites have been passed, in our search backward through time, the archeological record of artefacts becomes skimpy indeed. And, in the few cases where claims for such evidence are made, debates about authenticity continue for decades. But the evidence for technological behavior among living Primates suggests that this is one of many attributes which can be traced far into Primate prehistory. The ability to manipulate objects for specific purposes is probably one of the more ancient and pervasive trends in Primate evolution, having emerged perhaps as early as the Oligocene. Rudimentary kinds of modification and transportation, such as one sees today among baboon and chimpanzee collector-predators, may already have played a part in subsistence activities during the Miocene, although more sophisticated forms of such behavior, as performed by some contemporary human gatherer-hunters, may not have appeared until the Pliocene.

Most of the materials utilized by chimpanzees (and by other Primates) in their food-getting activities are highly maleable and perishable. These materials are in fact often indistinguishable, sometimes even after being modified, from similar materials to be found in the vicinity. Herein lie important implications for hypotheses which maintain that technological behavior initially arose among Primates when technical skills were applied to ‘hard’ materials that are prone to long-term preservation. Debates about the authenticity of the osteodontokeratic culture may continue for many years, but the likelihood that some extinct Primates once possessed technological capabilities—expressed for perhaps millions of years only in the manipulations, modification and transportation of ‘soft’ materials—is at least circumstantially strengthened by the chimpanzee evidence.

Final, unequivocal proof for such speculation must, of course, come from the discoveries of paleoanthropologists.

The approach which has been taken in this report—wherein acquisition and propagation of technological behavior is viewed as a gradual evolutionary process involving many Primate species—is offered for consideration largely because it appears to be theoretically more satisfying than those which link major evolutionary developments to some single factor (e.g. hominization to predation). Consequently, it is at least concordant with the incremental and cumulative processes of gradual change upon which biological theories of Primate evolution are founded. Hopefully my investigations have also shown that studies of nonhuman Primates can be relevant and instructive to those who seek knowledge about the emergence and evolution of *Homo sapiens*.

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